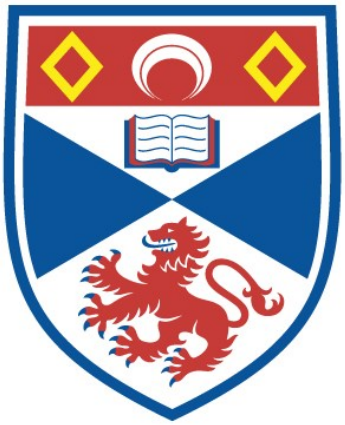
A CRITICAL EVALUATION OF THE FLORISTIC LINKS BETWEEN CHACO AND CAATINGAS VEGETATION IN SOUTH AMERICA

Darien Eros Prado

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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"Eu não sei mais nada.
Vou ter que começar de novo"

Prof. Dárdano de Andrade-Lima, back
in Brazil after his visit to the Chaco of
Argentina and Paraguay and shortly
before his untimely death.

[Prof. Severino do Monte Prazeres, pers. comm.]

To Fe and Eros, my beginnings and my principles
To Marta, my life
To Efraín, my future
To Paul Lewis, my mentor

I, **Darién Eros Prado**, hereby certify that this thesis has been composed by myself, that it is record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree or professional qualification.

Signed.....Date.....

I was admitted to the Faculty of Science of the University of St.Andrews under Ordinance General Nº 12 in October 1986 and as a candidate for the degree of Ph.D. in October 1987.

Signed.....Date.....

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the Degree of Ph.D.

Signature of the Supervisor.....Date.....19th August 1991

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ABSTRACT

The present study critically evaluates the alleged close floristic links between Chaco and Caatingas vegetation in South America. A reassessment of the phytogeography of these areas has been made by (a) comparing species lists in virtually all of the available literature, and (b) plotting dot-map distributions of relevant taxa based on the author's own herbarium studies and recent monographs. The environmental factors, geology and geomorphology, climate and soils of both areas were also analyzed to assess their degree of internal coherence. The prevailing concept of the Chaco itself proved to be a broad geographical entity rather than a well defined geobotanic unit in vegetational terms, and a redefinition of the Chaco *sensu stricto* and a new map of the province has been proposed. Several forest communities have been excluded from the Chaco *s.s.* since their floristic composition clearly link them to other neighbouring provinces. Although the Caatingas province vegetation is not so well known, the area appears to be a consistent natural region, and a new vegetation type has been briefly described.

Detailed floristic lists of the main woody and succulent species of the Chaco *s.s.*, the Caatingas and the Subandean Piedmont Forests are presented, which provide the basis for a subsequent phytosociological analyses (classical and numerical approaches) of these vegetation units vis-à-vis the rest of the seasonal forests and woodlands of South America. The results suggest that the alleged affinities Chaco-Caatingas are very feeble indeed, particularly when they are compared to the actual links between the Caatingas and other seasonal communities in the continent: the Guajira province in N Colombia and Venezuela, the dry forests of W Ecuador, and very particularly the Subandean Piedmont Forests in NW Argentina and SW Bolivia.

Some basic patterns of distribution of the floristic elements of seasonal forests in South America have been identified and found to form coherent trends in a series of accurate dot maps: a) Chaco endemics; b) Caatingas endemics; c) Neotropical seasonal forests pattern, including c.1- Residual Pleistocenic Seasonal Formations Arc (or 'Pleistocenic Arc'), extending from the Caatingas through some Planalto forests and calcium-rich localities in the Cerrados, SW Mato Grosso do Sul and the

Santiago and Chiquitos Sierras, to the Paraná-Paraguay river system and the Subandean Piedmont Forests; c.2- Tropical and Subtropical Seasonal Forests in South America; and c.3- Amphitropical Seasonal Forests pattern. The zoological evidence regarded until present as further proof of the Chaco-Caatingas links is also analyzed and mapped, and the results are sharply coincidental with those found for plant distribution.

An attempt has also been made to interpret the origin of the Caatingas flora; a hypothetical framework of probable ancient connections across South America between present-day seasonal woody communities is postulated, which have been interpreted here as migratory routes during the wet-dry climatic fluctuations of the late Pleistocene (18-12 ka BP). It is therefore concluded that the floristic links between the Chaco and the Caatingas are very weak and negligible when compared to other relationships, such as those between Chaco-Monte or Caatingas-Subandean Piedmont Forests. It is proposed that the Caatingas should be removed from the Chaquenian Dominium and placed in the Amazonian Dominium, with which they show much stronger affinities.

1. INTRODUCTION

Many authors have drawn attention to the physiognomic, floristic and faunistic connections between the Caatingas of NE Brazil and the Gran Chaco region of Bolivia, Paraguay and Argentina (Fig. 1.1), e.g. Smith & Johnston (1945), Beard (1953, p. 195), Andrade-Lima (1954, 1964a, 1967, 1981, 1982), Castellanos (1958), Rizzini (1963, 1979), Veloso (1964), Schnell (1966), Veloso & Strang (1970), Müller (1973), Vanzolini (1974, 1976), Bigarella et al. (1975), Short (1975), Cabrera (1976), Webb (1978), Cabrera & Willink (1980), Bucher(1982a), Prance & Schaller (1982), Ratter (1984), Haffer (1985), and Ratter et al.(1988b). For the most part the alleged floristic links comprise pairs of species (presumed vicariads), present in Chaco and Caatingas, such as *Ziziphus mistol - Z. joazeiro*, *Schinopsis quebracho-colorado - S. brasiliensis* , *Copernicia australis - C. cerifera* , *Aspidosperma quebracho-blanco - A. pyrifolium* , *Caesalpinia paraguariensis - C. pyramidalis/bracteosa* . A number of genera common to the two areas have also been cited: *Croton* , *Bumelia* , *Capparis* , *Mimosa* , *Acacia* , *Maytenus* , etc. . Furthermore, some of the above mentioned authors cite Hueck (1972) as having remarked on the impressive degree of physiognomic similarity of the Chaco and Caatingas, and also for a list of disjunct species with large populations in the two areas (Andrade-Lima, 1982). However, from a careful reading of Hueck (1972) the only relevant observations with regard to the physiognomy of the Caatingas seem to be his comment: "Na sua aparência lembra principalmente as matas do Chaco do centro da América do Sul" (p. 309). And describing typical Caatingas forest Hueck wrote: "El aspecto del bosque recuerda mucho al bosque seco del Chaco" (Hueck, 1959, p. 9). These casual references to physiognomic similarities seem to have been transformed into deep floristic relationships.

Cabrera & Willink (1980) included the Chaco and Caatingas, together with the Espinal, Monte, Prepuna and Pampean provinces, in their 'Chaquenian Dominium'. According to these authors, this Dominium was quite homogeneous and characterized by the predominance of Leguminosae (*Prosopis* , *Acacia* , *Caesalpinia* and *Cercidium*), Zygophyllaceae (*Larrea* , *Bulnesia* and *Plectrocarpa*), Anacardiaceae (*Schinopsis* and *Lythraea*), Rhamnaceae (*Ziziphus* and

Fig. 1.1: Position of the Gran Chaco and the Caatingas in South America.

Scutia), Capparidaceae (*Capparis* and *Atamisquea*) and numerous genera of Bromeliaceae and Cactaceae. However, only five out of these 13 genera can be actually found in the Caatingas: *Acacia* , *Caesalpinia* , *Capparis* , *Schinopsis* and *Ziziphus* , and the other genera have been excluded from that province in all of the most detailed surveys of caatinga vegetation (Luetzelburg, 1922-23; Egler, 1951; Andrade-Lima, 1954, 1960 & 1981; Figueiredo Gomes, 1981;Emperaire, 1983; Carvalho, 1986). Against this background the present study has aimed to attempt a more critical evaluation of the floristic links between these two areas.

Axiomatic to any study of 'floristic similarity' is the question of what is a phytogeographical province as an abstraction. In this study, the concept proposed by Braun-Blanquet (1919, *sub* 'Domaine'), later modified by Takhtajan (1986), is followed. This system consists essentially of the subdivision of the World flora into areas ordered in hierarchical categories according to their degree of floristic endemicity and their 'taxonomic' rank. Thus, the system comprises 'kingdoms', characterized by endemic families, subfamilies and tribes; 'regions', established on the basis of high numbers of generic and specific (and sometimes even small family) endemisms; 'provinces' are subdivisions of the regions in which generic endemism is less relevant and usually consists of a reduced number of monotypic or oligotypic endemic genera, but in which specific endemisms are abundant and characteristic; the lowest category is the 'district', mainly established by subspecific endemism and where specific endemism is absent or weakly expressed (Takhtajan, 1986). Castellanos & Pérez-Moreau (1944) widened the 'province' to an ecological concept, such that it has to comprise not only the characteristic generic and specific endemics but also several edaphic communities and at least one climax community.

It is important to note that phytogeographical provinces do not necessarily coincide with geographical regions which may bear the same name. Thus, in South America the geographical areas denoted by Pampa, Monte, Caatingas, Patagonia, Amazonia or Chaco do not imply a homogeneous vegetation or equivalence with phytogeographical provinces. The danger of the misuse of geographical regions as synonyms of vegetation units has been pointed out by Castellanos & Pérez-Moreau (1944) for the Argentine vegetation and emphasized by

Castellanos (1960), and also as regards the Brazilian vegetation by Kuhlmann & Correia (1982).

To assess the degree of relationship between Chaco and Caatingas the following approaches were adopted in the course of this study:

a- An exhaustive search of the literature for floristic lists and phytogeographical observations on both areas and related ones was carried out.[1]

b- The present author has accumulated field experience for parts of the Chaco, based on many ecological and floristic surveys carried out from the University of Rosario (Argentina) in areas of Santa Fe, Córdoba, Chaco and Santiago del Estero provinces, and subsequent surveys in riverine vegetation in the river Paraná valley and tributaries.

c- During the course of this thesis further brief but very important fieldwork in NE Brazilian Caatingas (Pernambuco and Ceará states) was undertaken. The core Cerrado area near Brasilia and calcareous forest remnants in the Federal District were visited, and also similar outcrops around Corumbá in Mato Grosso do Sul. A preliminary survey of the alleged Chaco intrusion in the latter area was carried out.

d- An exhaustive check on taxonomic literature and verification of identity of those species cited in floristic lists and phytogeographic accounts was made by repeated visits to Royal Botanic Gardens, Kew and RBG Edinburgh, and also with exsiccata obtained on loan from various Herbaria.

e- Elaboration of a series of accurate distribution dot maps based only on verified specimens or on trustworthy modern revisions (solid black dots), and also on citations in reliable vegetation surveys of the areas involved (open circles).

f- Statistical (numerical) analysis of floristic lists on a basis of presence-absence of species was performed (Complete Linkage Algorithm-CLINK, in Wishart, 1987, and Principal Components Analysis-PCA, in JUMP IN™), and this compared to classic phytosociological analysis (Braun-Blanquet modified by Mueller-Dombois & Ellenberg, 1974).

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[1] Abundant references to be found in the Chaco and Caatingas chapters (Ch. 2 & 3).

g- Finally, an attempt was made at a synthesis of the biogeography of certain parts of South America linked by related types of dry vegetation which form an arc across the continent.

2. THE GRAN CHACO VEGETATION

Within the framework of Southamerican phytogeography the term Chaco or Gran Chaco has been applied to the vegetation covering the vast plains of north-central Argentina, western Paraguay and SE Bolivia, and entering into Brazil as a narrow strip parallel to the river Paraguay in Mato Grosso do Sul (Fig. 1.1). Covering about 800,000 km^2 (Hueck, 1972) or 1,000,000 km^2 (Bucher, 1982a), it is one of the few areas in the world where the transition between the tropics and the temperate belt does not occur in the form of a desert but rather as semiarid forests and woodlands (Morello & Adámoli, 1968). For most authors the Chaco phytogeographical province has simply been equated with the Chaco Geographical Region, as shown in Hauman (1931), Kanter (1936), Ragonese & Castiglioni (1970), Cabrera (1953, 1971, 1976), Morello & Adámoli (1968, 1974), Hueck (1972), Hueck & Seibert (1981), and Zellweger et al. (1990), and no attempt has been made to date to critically evaluate the homogeneity of the resulting vegetation.

In the following sections the environmental factors modelling the vegetation of the Gran Chaco, and the floristics and structure of the vegetation itself, will be analyzed. The actual geographical area encompassed by this analysis corresponds to the broadest one, i.e. that of Ragonese & Castiglioni (1970). They described the plant cover extending from the gallery forests on the islands of the river Paraná in the east to their 'Subandean Sierra Chaco' in the west (which seems to be simply an impoverished version of the 'Palo blanco' forest). The rationale of choosing the broadest possible concept as starting point for this analysis arises from the need to take into account every vegetation unit susceptible to being regarded as chaquenian, and then test the validity of its inclusion within the province vis-à-vis both the core area of the Chaco itself and the rest of the South American phytogeographical framework. The present-day most widely accepted concept of the phytogeographical province is that of Cabrera (1976), that is to say from the forests close to the river Paraná in the east (but excluding the gallery forests and 'Selva de ribera' units), to the Sierra Chaco in the west (but excluding the 'Palo blanco', i.e. the so-called Transitional forests). There are other relevant but not widely accepted ideas of what the Chaco is, such as that of Hueck (1972) which simply includes the 'Palo blanco'

unit. The limits set by Ragonese & Castiglioni for the 'Chaquenian Park' (1970) most closely equate with the Chaco Geographical Region as defined by Kanter (1936). The map of the Chaco region in Morello & Adámoli (1968) is a similar case. These latter authors nevertheless provide the most useful phytogeographical subdivisions of the Chaco to date (Fig. 2.1), which were later slightly modified by Marlange (1972).

2.1- The usage of the word Chaco:

In all likelihood the word 'Chaco' is from quechua origin. When the first Spanish Conquistadores arrived to present-day Peru, the quechua-speaking Inca civilization used the term 'chacu' or 'chaku' to designate the method of hunting by surrounding a piece of land with a large number of natives, shouting and producing noises so as to frighten the game and progressively closing the circle. Cobo (1964, p.269) described a 'chacu' involving some 10,000 indians and spreading over leagues of land in honour of Pizarro by mandate of Manco Inca. This meaning has been widely accepted by most scholars (Middendorf, 1890; Lira, 1942; Castellanos & Pérez-Moreau, 1944; Métraux, 1946; Morínigo, 1966) and by the Dictionary of the Royal Academy of Spanish, and usually accepted in a shortened version as 'hunting land'.

However, it seems that the Inca dominium never spread into the geographical Chaco or if it did it was very sporadically and in short-lived settlements, since archaeological evidence is very scarce and of arguable origin (Métraux, 1946; Fock, 1961). By contrast, the vast plains of the Chaco were roamed by war-like semi-nomadic hunter-gatherer aborigines, whose fierceness prevented white-man settlements until late XIX century in certain parts of the Argentine Chaco and the first third of this century in Paraguay and Bolivia. Their languages pertained mainly to the Zamucoan, Matacoan, Guaicuruan, Mascoian and Lule-Vilelan language families, rather than Quechua (Métraux, 1946). How is it then that the name 'Chaco' was so widely used for this area since early colonial times in South America?. The jesuit Camaño (1955) provided the most likely and logical explanation: the quechua-speaking indians of Humahuaca (in NW Argentina) used to go hunting in the plains east of their mountainous country; the Spaniards, who came from Peru to NW Argentina to found the oldest cities of that country, must have enquired what lay further to the east, and the answer 'chacu' -and

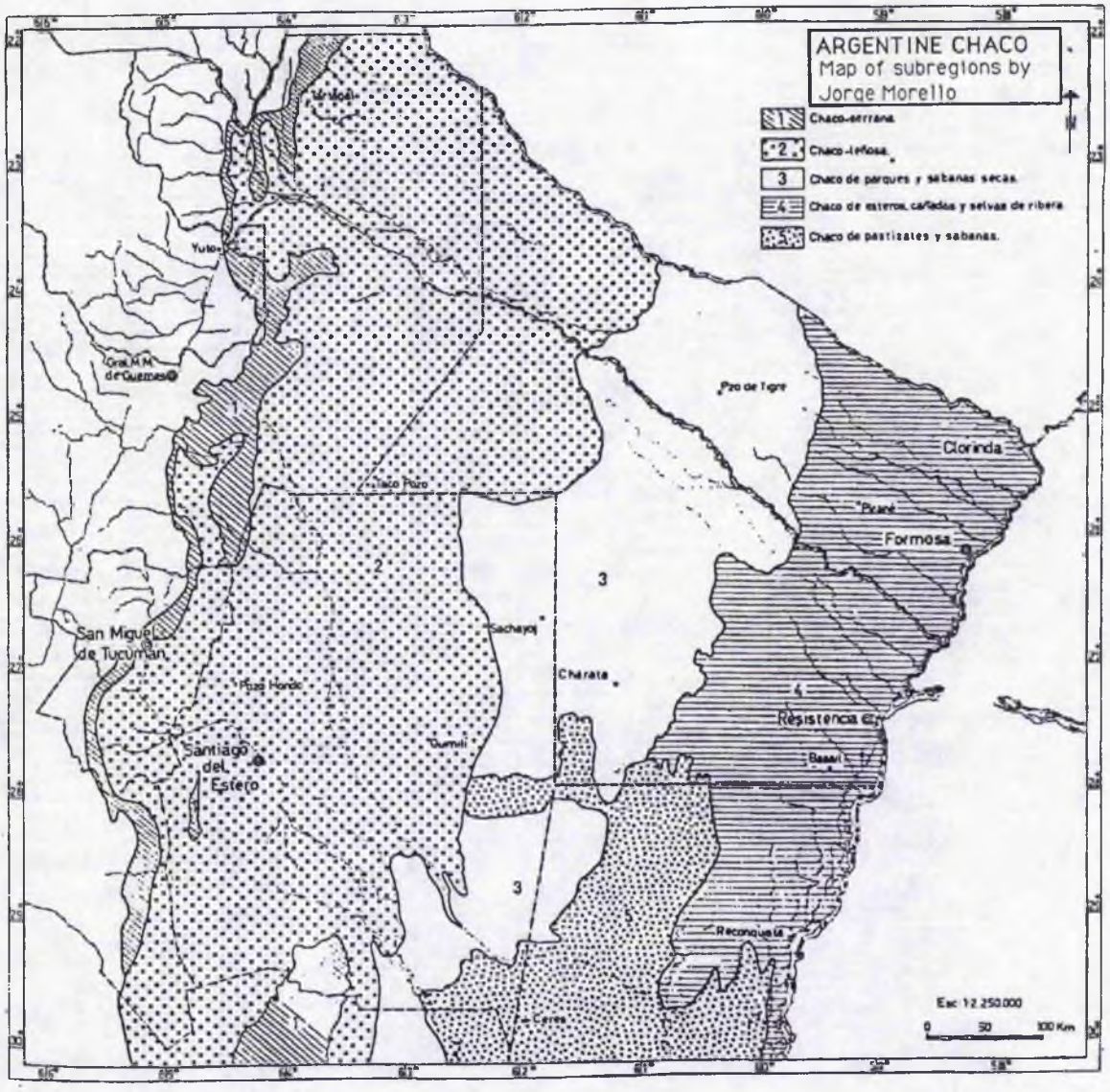

Fig. 2.1: Subregions of the Argentine Chaco. Modified from Morello & Adámoli, 1968.

subsequently by mispronunciation: 'chaco'- was believed to be the name of those lands. When finally the first Spanish colonies were established on the margins of the Paraguay and Paraná rivers, which are the actual eastern borders of the geographical Chaco, the name had already spread throughout the River Plate Dependencies to designate the lands east of the Subandean and Pampean chains, south of the Santiago and Chiquitos ranges in Bolivia, north of the treeless Pampas and west of the rivers Paraná and Paraguay.

This last eastern limit proved most difficult to colonize and it was not until nearly 1880 that the first contingents of immigrants founded Resistencia and Formosa cities on the W margin of the Paraná and Paraguay rivers respectively. This protracted stage of *terra incognita* must have helped cement the concept of the Chaco Geographical Region as a unit, which is a very useful abstraction from the anthropological, economic and administrative point of view (see for example the study by Morello, 1985), but not necessarily so as regards the phytogeography of the continent.

2.2 (a)- Geology and geomorphology:

The topography of the Chaco shows an amazing monotony all over the region, with some low-height elevations towards the western limit in Argentina and Bolivia, and also in a sector of the Paraguayan-Bolivian border (Ramella & Spichiger, 1989); the terrain is nearly horizontal, thus provoking the only three rivers crossing the Chaco (all of them aloctonous) to meander, and at the same time to have laterally fluctuating courses[1] within an up to 100 km wide flat valley covered with abandoned ox-bows.

Perhaps the most characteristic feature of the geomorphology of the Chaco-Pampean plains is that they consist of a massive accumulation of Quaternary sediments over the deeply sunk Pre-Cambrian Brazilian Shield. These sediments are the result of the erosion of the at that time recently risen Andes, which were transported æolically to the southern half of the Chaco geosinclinal (therefore called Chaco-Pampean loess or loessic sediments), or æolically but mainly

[1] For example, geomorphologists have detected at least five changes of course of the Salado river (Castellanos, 1968), and its bed fluctuated of position once in this century.

hydrologically to the northern half of the Chaco trough, to form the scarcely known 'Chaco sediments' of the Paraguayan Chaco (Putzer, 1962). These plains must have originated as a vast sedimentary basin in the Palæozoic, extending further east than today over the Pre-Cambrian Shield (Fig. 2.2a). From the beginning it had a tendency to subside (Popolizio et al., 1980a), and the pressure of the successive layers of sediments provoke the crystalline base to fracture in smaller blocks with a general NE-SW direction (Fig. 2.2b). During the Tertiary these blocks moved differentially; the Argentinian Mesopotamia and eastern Paraguay started to rise (Teruggi, 1970), thus putting an abrupt eastern border to the Chaco plains, while in the W the Subandean Sierras were formed as an even more straightforward limit. In the middle of the plains, a line of blocks rose forming what today is known as the Charata-Eastern Córdoba Arc or Dorse (Padula & Mingramm, 1963) (Fig. 2.2c), which divides the area in two geomorphological basins, Alhuampian and Chaquenian. During the Quaternary the modern features of these plains were settled with the deposition of massive loessic sedimentary layers, obliterating most of the previous relief caused by the movements of the crystalline blocks (Fig. 2.2d). The Pampean loess is missing over the north of Argentine Mesopotamia and eastern Paraguay (Teruggi, 1970).

The differential block movements in the same NE-SW direction (Brazilian alignment) spread not only in the Argentine Chaco but also in the Paraguayan, as shown in Putzer's geological map (1962). In NW Paraguay the Brazilian alignment of fractures meets a Caribbean one (NW-SE direction), this allowing for a much deeper fault movement of over 1000 m (Putzer, 1962) which created the tectonic horst of the Cerro León area. This block, basically formed by Lower Devonian and Silurian outcroppings, has risen up to 720 m above sea level (Ramella, in litt.). There are some other isolated hills near the Cerro León area which generally share a common tectonic horst genesis, such as the Cristián, Cabrera, Caimán and San Miguel tableland hills, of which the latter is the highest point within the expanse of the Chaco (Ramella & Spichiger, 1989). Thus, it is clear that the sparse relief basically originated from an underlying horst and graben structure covered by a thick sedimentary layer, and that the Chaco comprises true plains caused by accumulation. The Chaco plains cannot be regarded as peneplains as claimed by Ramella & Spichiger (1989), i.e. extensive piedmonts caused by erosion

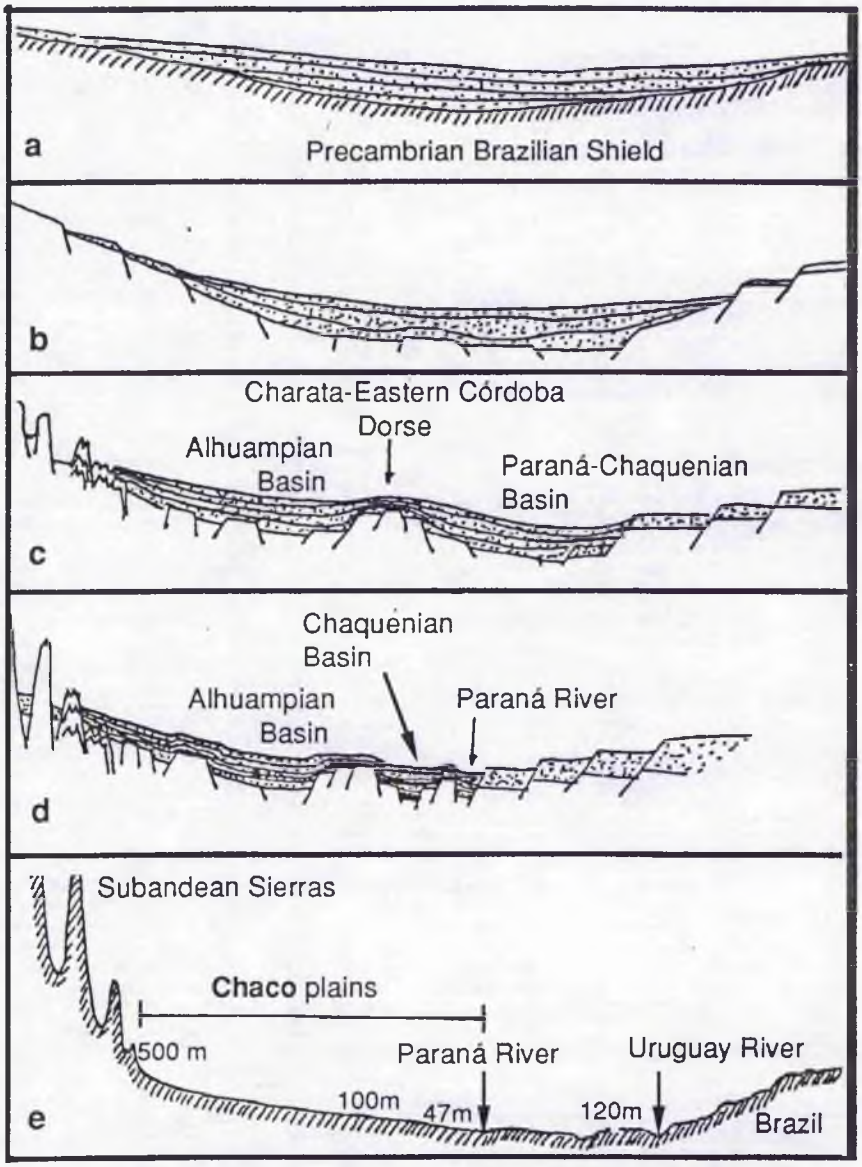

Fig. 2.2: Geological origin of the Chaco plains (see explanation in text). Modified from Popolizio et al., 1980a .

and removal of massive amounts of material; there is absolutely no evidence of such a process in the Chaco, where no glacis or inselbergs can be found. The origin of the localized palæodunes fields in W Paraguay and E Bolivia is also debatable; this author believes they can hardly have originated from fluvial transport and accumulation (cf. Ramella & Spichiger, 1989), but rather they must be the remnants of a much drier period probably caused by Pleistocenic climatic fluctuations such as those which formed the palæodunes fields of the middle São Francisco river valley in the Caatingas (Tricart, 1985). Such fluctuations did occur in the northern Chaco where the draining system of a more humid period during the Pleistocene, which left behind the youngest sedimentation to be found, is recognizable from the air (Putzer, 1962).

Popolizio et al. (1980a) divided the Chaco region in four major morphogenetical units, from west to east: a) *piedmont chaco* , in transition with the western mountainous ranges and in the shape of a narrow fringe along them; b) *bajada chaco* , over a huge alluvial apron of extinct rivers and which is under the influence of a semiarid subtropical modelling system; c) *western chaco plains* , coinciding with the slightly elevated Charata dorse; d) *eastern chaco plains* , under a humid, with no dry season, subtropical modelling system on mainly recent alluvial deposits from the Paraguay-Paraná axis. This last unit is the only one with autochthonous rivers, which are still modelling the surface in a dendritic net unique in the Chaco region, and this fact together with the scarce energy of the relief, soils with impeded drainage and higher rainfalls, provoke the unit to undergo the effects of waterlogging, floodings and marsh formation.

2.2 (b)- Climate:

The highest absolute temperatures in South America have been registered in the Chaco. Prohaska (1959) referred to the area encompassed by the 47°C isotherm of absolute maxima as the 'South American Pole of Heat' (Fig. 2.3). Nevertheless, this very hot summer with maxima up to 48.9°C is associated with frosts in winter (Galmarini & Raffo del Campo, 1964). In fact, apart from a narrow fringe in the east and parallel to the major rivers, no point within the Chaco geographical region is free from frosts, their average frequency ranging from nearly 0 in the east to 11.3 days or more in the west (Marlange, 1972). Consequently, there is also an east-west gradient with regard to the

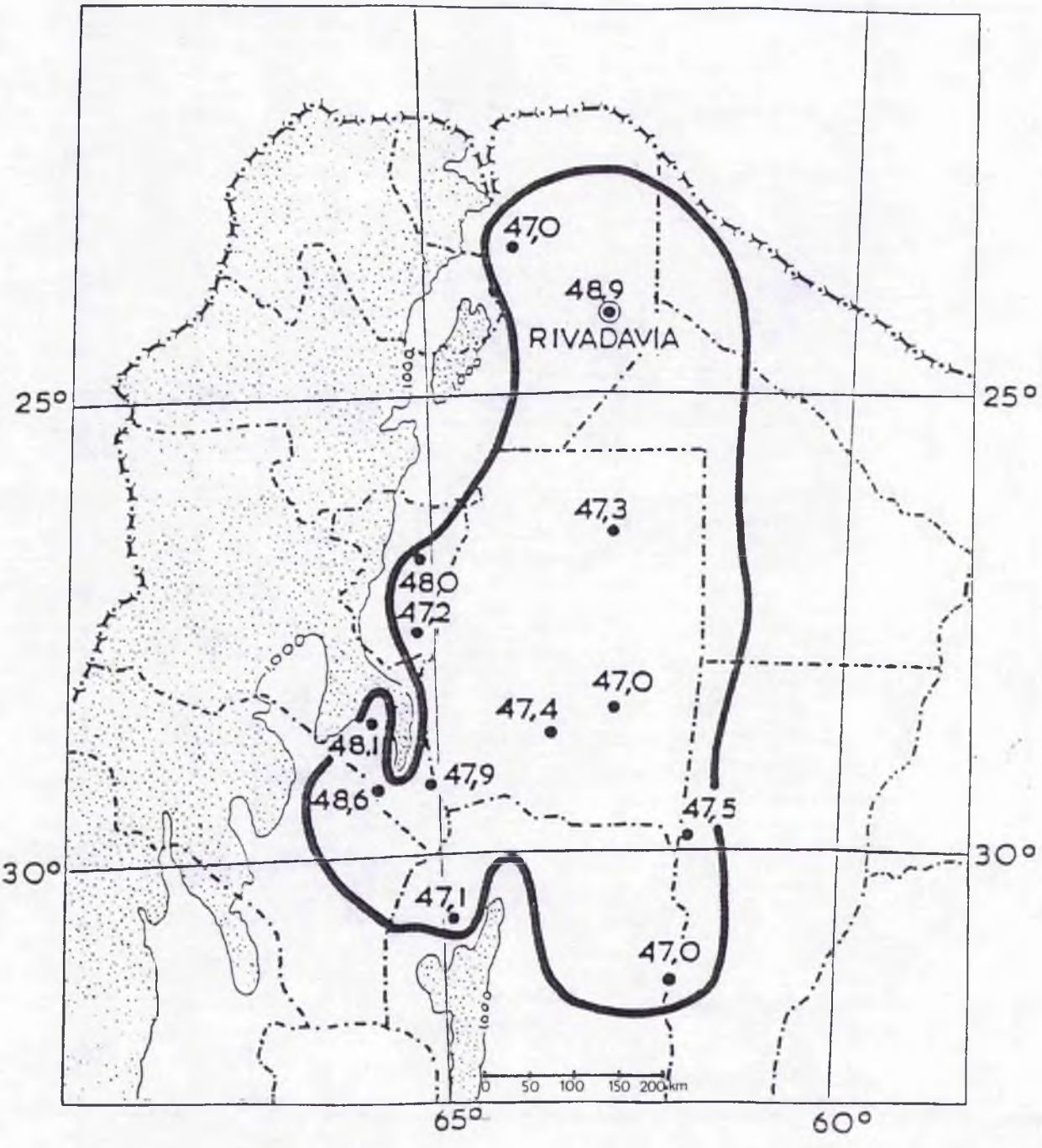

Fig. 2.3: The 'South American Pole of Heat', according to Prohaska (1959). Modified from Galmarini & Raffo del Campo, 1964.

lowest absolute temperatures, from -1.1°C in Corrientes to -7.2°C in Santiago del Estero. In contrast, the mean annual temperature varies in a north-south latitudinal effect from about 26°C in N Paraguay (Fariña Sánchez, 1973; López Segovia et al., 1988) to 17°C or less in the hills of the Sierra Chaco (Ragonese & Castiglioni, 1970).

The map of Fig. 2.4 shows the isolines of precipitation, extracted from Galmarini & Raffo del Campo (1964). Again there is an outstanding E-W gradient from 1267 mm in Formosa city to 514 mm in Rivadavia, and down to about 350 mm in Catamarca or La Rioja in the extreme W and SW of the Chaco. There is a manifest yearly variation in rainfall, with a strong, marked dry season in winter-spring, and a rainy season from October to April; the length of the dry season increases markedly from E to W, with no dry month in Formosa (Papadakis, 1973) to 6 months with negligible rainfall in Rivadavia in the Salta province, or in Catamarca or La Rioja. In the western limit of the area there is a sudden inversion of the rainfall gradient as a result of the cooling of the warm air masses, which cross the plains and lose most of their humidity in the eastern third as they encounter the first heights in the western border of the Chaco (Pampean Sierras in the S, Subandean Sierras in the N). Thus, there is a moderate increase of rainfall in the Pampean Sierras (owing to their relatively low altitude) from about 500 mm in the nearby plains to over 700 mm, and a more dramatic one along the eastern slope of the Subandean Sierras from the province of Tucumán to the north. In this latter case the first low hills to the east, although not high enough to generate orographic rains, benefit from the effect of the mountains to the west and receive up to 800 or 900 mm/year (Sarmiento, 1972). Further away from the plains height has increased from about 500 m to 2000 m or more, and with it rainfall rises from 900 mm up to 1500 or even 2000 mm (Groeber, 1958). Again there is a marked drop in rainfall in the rain-shadow slopes of the subsequent ranges of mountains, resulting in dry west-facing slopes (700 mm down to 300 mm) as opposed to humid east-facing slopes in the same valleys (up to 1500 mm) (Hueck, 1954; Sarmiento, 1972).

Although the general E-W rainfall gradient of the Gran Chaco is a well-known fact, it is not a gradual and steady decrease. In Table 2.1

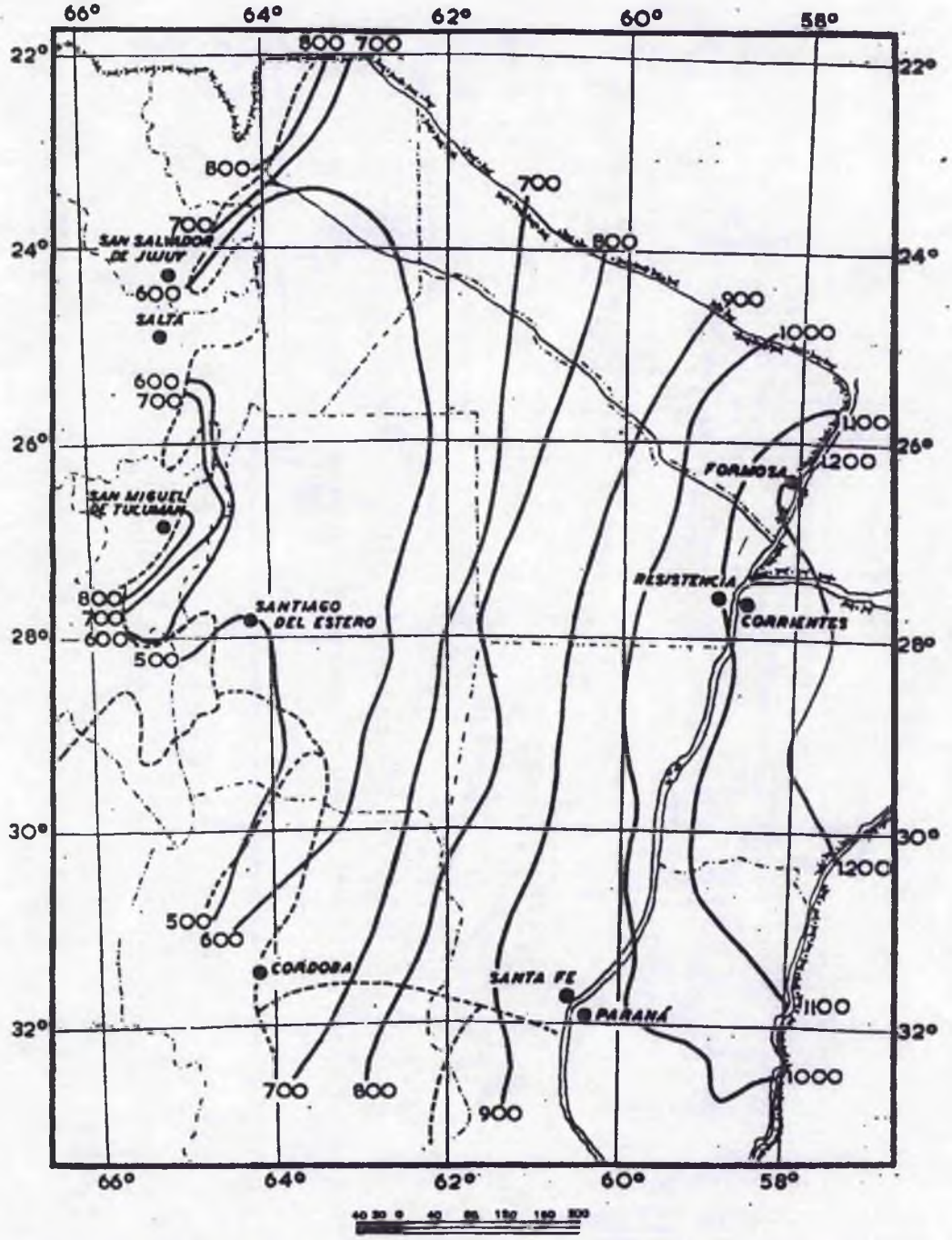

Fig. 2.4: Rainfall isolines for the Argentine Chaco. Modified from Galmarini & Raffo del Campo, 1964.

TABLE 2.1: **Rate of decreasing rainfall (mm/km) in two W-E transects across the Gran Chaco (data from Galmarini & Raffo del Campo, 1964, and Boletta, 1988).**

a)	WEST					EAST
Locality	J.V. GONZÁLEZ	RIVADAVIA	ING. JUÁREZ	POZO DEL TIGRE	PIRANÉ	FORMOSA
Rainfall (mm/year)	539	514	672	858	1027	1267
Appr. distance (km)	165.00	107.50	178.75	157.00	100.00	
Decreasing rainfall rate (mm/km)	0.15	-1.47	-1.04	-1.08	-2.40	

b)	WEST					EAST
Locality	CRUZ DEL EJE	SANTIAGO D. ESTERO	CAMPO GALLO	CORZUELA	PRES. DE LA PLAZA	CORRIEN-TES
Rainfall (mm/year)	481	554	580	799	985	1186
Appr. distance (km)	322.50	142.50	180.00	110.00	100.00	
Decreasing rainfall rate (mm/km)	-0.23	-0.18	-1.21	-1.69	-2.01	

two E-W rainfall transects are shown, with data from Galmarini & Raffo del Campo (1964) and Boletta (1988). In the first case, since the localities are nearly at the same latitude, distances shown are measured on a straight line uniting each pair of localities; in the second case an imaginary line uniting Corrientes with Santiago del Estero was drawn, and distances measured where it intersects with the meridian corresponding to each locality. In both cases the decreasing rainfall rate shows a dramatic fall in the first 100 km of over 2 mm/year for every km to the west, but once deeply within the Chaco, the rate decreases only gradually to reach virtually zero values in the far west of the region.

Potential evapotranspiration decreases southwards from 1150 mm to 900 mm, but increases westwards up to 1200 mm in the centre of western Chaco, to decrease again near the mountainous ranges with very close isolines. A sharp fall in Moisture Index values (*sensu* Box, 1986) from east to west would be expected as a consequence, and this is confirmed by his figures and also by Papadakis' Hydric Index (1973) values across the area. It should be pointed out that the critical MI=1 isoline, the hypothetical boundary between humid and dry climates, when using the Thornthwaite potential evapotranspiration estimate, runs parallel to the meridians and puts most of Eastern Chaco on the humid side (Box, 1986).

2.2 (c)- Soils:

The parent materials of the Gran Chaco soils are fine sediments brought in by a æolian or fluvial transportation, or depositions of lacustrine or even Devonic marine ingressions sediments. In this context stones and pebbles are of extremely rare occurrence, and rock outcroppings are non-existent. Only a few exceptions occur and always in marginal areas close to the borders and linked to the western mountain ranges. One of the constant features of the soils across the area is their texture, since particles never go beyond 2 mm (Marlange, 1972); this characteristic is not only important because of its mechanical and physical implications, but also because whilst several pedogenetical elements vary from E to W (climate, vegetation), texture remains fairly constant. Thus, the kind of soil present is a direct result of the influence of the prevailing environmental factors, particularly climate.

As a consequence, there is an E-W gradient of climatogenic soil types; according to Bonfils (1970; also Bonfils, in Ragonese & Castiglioni, 1970) well developed Brunizem soils are present in a narrow strip parallel to the river Paraná on high topographic position. Espino et al. (1983) in their description of the soils of northern Santa Fe, and that of Ledesma (1973) for Chaco administrative province, coincide in assigning the most important soils of the eastern area to Brunizem with a clay textural B horizon through illuviation. Further inland, Grumosols and Reddish Chestnuts dominate the landscape, usually with an argillic B horizon, and associated to Planosols and Solonetz together with others of the saline cycle. Towards the centre of the Gran Chaco, Regosolic Chestnuts are common, while in the western third of the region some aridic soils prevail, such as Cinnamon Chestnuts and finally Reddish Browns (Bonfils, 1970), associated with extended Alluvial soils in the NW and massive saline areas in the extreme SW. The Sierra Chaco is generally established on Lithosols in the Pampean Sierras, while in the northern Subandean mountains there are Alluvial soils in the bottoms of dry valleys, Lithosols on dry slopes and Forest Brown on the humid windward slopes (Bonfils, 1970). Vargas Gil & Vorano (1988) classified the Gran Chaco soils according to the 7th Approximation, but this does not alter the E-W gradient; they found typical Hapludols and Argiudols in the extreme east, Argiustols and Haplustols in the central area, and typical Haplustol, aridic Haplustol and aridic Haplustalfs in the west.

Some non-climatogenic soils also occur in the Gran Chaco. The overflowing of rivers, now extinct or severely diminished in their caudal, provided extensive layers of alluvial sediments (Putzer, 1962) to form a series of young and scarcely developed soils such as those in the Alluvial Salta Chaco in eastern Salta province (Adámoli et al., 1972). Alluvial Quaternary deposits also occur in the eastern third of the Formosa province soils. Planosols with a perched water table can be found in depressions all across the Gran Chaco, although hardly perceptible by topographic difference. There are extensive areas with soils of the saline cycle, and due to the arid and semi-arid climate soluble salts are abundant. Thus, Saline, Solonetz and Soloth soils are a common feature in low areas with poor drainage. The abundance of salts provokes an easy dispersion of clay, and the consequent heavy-textured sub-soils are prone to flooding in the rainy season (Beek & Bramao, 1968).

The Gran Chaco soils are poor in organic matter, and the humic horizon is relatively shallow; in the east it can extend up to 20 or 25 cm depth (Espino et al., 1973), but it nearly disappears in the west. Daily maxima temperatures are high even in winter, and this together with environmental dryness and scarcity of protective Graminae facilitates a very quick mineralization of organic residues (Papadakis, 1973). Parent materials and the mainly semiarid climate make mineral deficiencies very improbable, although ant mounds generate very localized sterile spots (Bucher, 1982a). There is usually a calcium carbonate-rich horizon, and nearly all soils give an increasing effervescent reaction to HCl from west to east (Papadakis, 1973). Hardpans of calcium carbonate and silica are frequent in the east of the Chaco. In Papadakis' view, the main set-backs of the soils of the Gran Chaco are poor drainage, salinity and alkalinity, flooding under occasional excessive rainfalls, and the presence of clay textured horizons or even hardpans in places.

2.3- Vegetation:

The plant cover of the plains of the Gran Chaco, considering its extension and the several environmental gradients already described, inevitably shows a certain degree of variability, although some general features might remain constant. The analysis will be carried out from east to west so as to follow the major environmental gradients, and it will be mainly focused on the Argentine Gran Chaco, for which there is abundant information coupled with field experience of this author. For the Paraguayan and Bolivian Chaco, and also for the Brazilian sector with allegedly Chaco vegetation, information is scanty and sometimes imprecise, but nevertheless some tentative conclusions can be reached. The geographical range of this study (see Fig. 2.5a & b) extends from the Paraguay and Paraná river valleys in the east to the western mountainous ranges, and from the Santiago and Chiquitos ranges in Bolivia to the peri-steppic Thorn Woodlands (Espinal Periestépico, *sensu* Lewis & Collantes, 1973, and Cabrera, 1976) in the south, which is actually an enormous ecotone Chaco-Pampa. Morello & Adámoli's (1968) subdivisions of the Gran Chaco will be followed and frequently referred to throughout this chapter, though with more simplified nomenclature. Thus, their 'Chaco de esteros, cañadas y selvas de ribera' along with the 'Chaco de pastizales y sabanas' (see Fig. 2.1)

Fig. 2.5a: Political divisions and main geographical features of the Gran Chaco area.

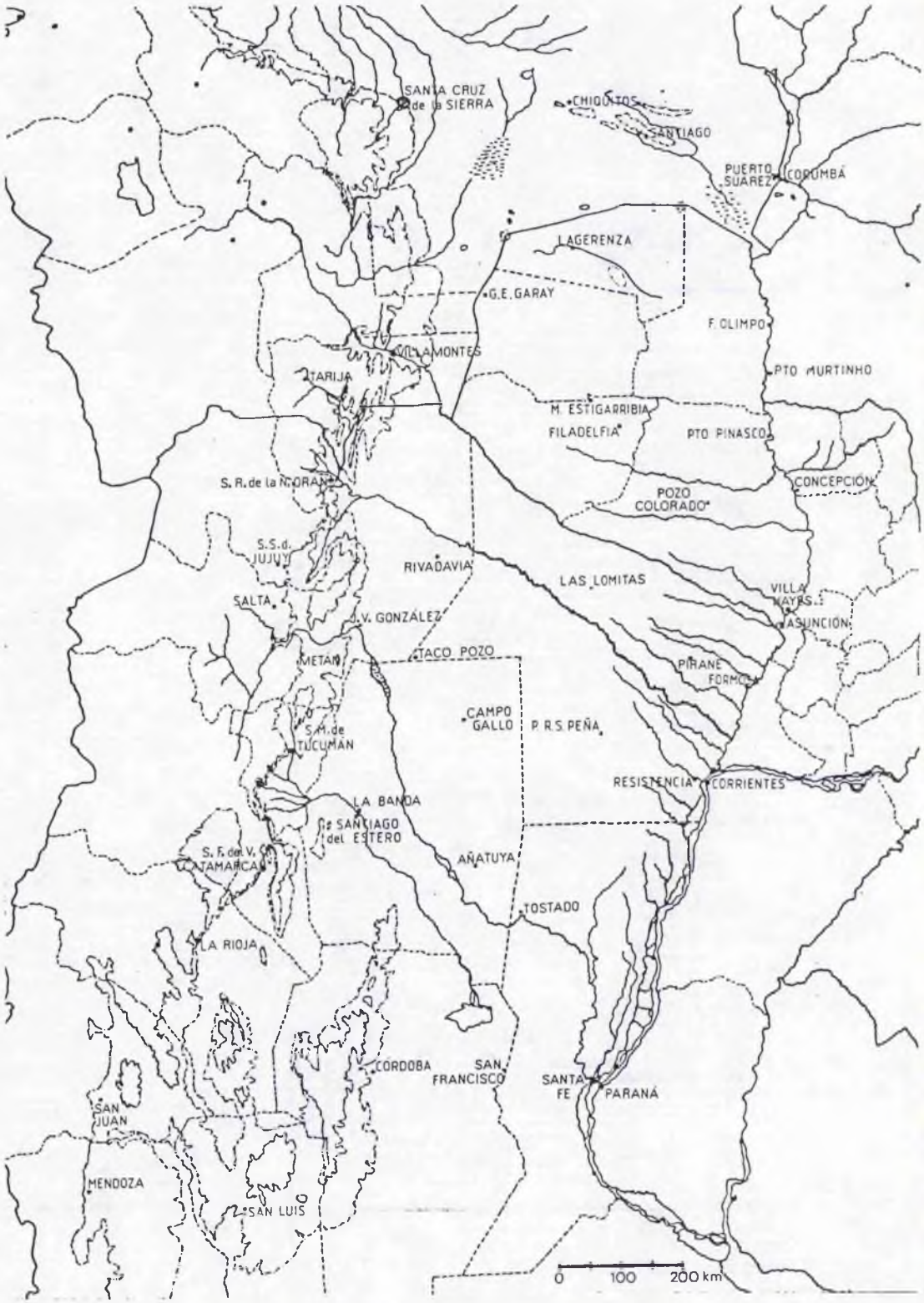

Fig. 2.5b: Some critical localities of the Gran Chaco area.

equals what here is called Eastern Chaco; their 'Chaco de parques y sabanas secas' will be referred to as Central Chaco; their 'Chaco leñosa' as Western Chaco; and the 'Chaco serrana' is equivalent to the Sierra Chaco. These equivalents are only used as convenient subdivisional names, but the vegetation or phytogeographical territories ascribed to them by these authors are not necessarily accepted.

In general terms the most peculiar feature of the vegetation of the Chaco consists of the dominance by species of the arboreal genus *Schinopsis* . In the humid, frequently waterlogged eastern plains the predominant species is the simple-leaved *S. balansae* ; in the dry and flat plains of central and western Chaco the most important tree is *S. quebracho-colorado* , with imparipinnate, linear-lanceolate, numerous leaflets. In the lower belt of the western Sierras the dominant species is *S. haenkeana* , which closely resembles the former but with ovate leaflets. Their vernacular names - 'quebracho' (from 'quiebra-hacha' or axe-breaker) - reflects the hard quality of their tannin-rich wood. Also characteristic are the forests of *Bulnesia sarmientoi* ('palo santo') in western Formosa and eastern Salta, and those dominated by *Aspidosperma quebracho-blanco* ('quebracho blanco') in the plains of eastern Catamarca, La Rioja and San Juan, NW San Luis and W of Córdoba in Argentina (Ragonese & Castiglioni, 1970).

However, forests and woodlands are not the only feature of the Gran Chaco, since savannas are also a very important component of the landscape: *Elionurus muticus* savannas with scattered *Prosopis* spp. trees are common throughout the region; *Spartina argentinensis* savannas, with or without trees, have been extensively studied by Lewis et al. (1990a & b). Palm savannas and palm-tree woodlands of *Copernicia alba* are very important and sometimes dominant in the landscape from the Brazilian Pantanal to NE Santa Fe in Argentina, always on alluvial, seasonally flooded ground under the influence of river systems in the east of the region. Such savannas are not evenly distributed across the Gran Chaco and there is an evident decreasing frequency of savanna physiognomy towards the west, as the subregional names by Morello & Adámoli (1968) clearly show (Fig. 2.1). This is why, as already stated by Morello & Adámoli (1974), it is certainly improper to denominate this region as Chaquenian Park ('Parque Chaqueño'), as employed by Parodi (1945), Cabrera (1953) and Ragonese & Castiglioni

(1970), since although this physiognomy is frequent and in areas dominant, it is not the case for the whole of the Gran Chaco.

A number of woody communities can be found in each sector, some of which are exclusive to it and some others, with minor variants, are roughly the same throughout the three main sectors of the Chaco. In dealing with every sector only the exclusive communities will be described, while the more generalized ones will be dealt with under the heading 'Azonal woody formations'. In Table 2.2 an attempt has been made to fit the main chaquenian woody communities into Beard's (1955) system of vegetation physiognomy, and this is compared with Sarmiento's (1972) nomenclature when available. Since Beard's system was designed for tropical vegetation, the term 'subtropical' should be added before his classes in this table.

2.3.1- Gallery Forest:

The islands in the river Paraná, together with the banks of the river Paraguay and their western tributaries, present a peripheral levee ('albardón') above the level of waters except for the flooding season, which is formed by the deposition of coarse materials brought in by the river floods. The vegetation is usually a forest up to 20 m high, which is floristically rich although it is in effect an impoverished version of the Subtropical Rain Forests of Misiones (Argentina), southern Brazil and eastern Paraguay (Cabrera, 1970; Sarmiento, 1972; Klein, 1972; Cabrera, 1976). It comprises up to three tree strata and is rich in lianas, ferns and vascular epiphytes (Ragonese, 1941), and the species not rising above the middle storey are evergreen. This forest is subject to yearly floodings from the nearby rivers and this strongly determines the floristic composition, e.g. as the presence of Lauraceous trees and several other species found only in this kind of community demonstrates (see Ch. 6, Table 6.1 for a typical example). Following the courses of the tributaries such forests may penetrate up to 100 to 150 km into the Gran Chaco plains. Good descriptions of this formation can be found in Burkart (1957a), Franceschi & Lewis' *Forestum Nigrum* (1979), Franceschi et al. (1985) and Eskuche (1986). Morello & Adámoli's (1974, p.108) 'bosque alto o selva de inundación' corresponds to this unit as well.

TABLE 2.2: **Physiognomy classes equivalences for the main woody communities of the Chaco and neighbouring formations.**

	BEARD (1955)	SARMIENTO (1972)
Gallery forest	Semideciduous Seasonal Forest	Deciduous Rain Forest
Selva de Ribera	Semideciduous Seasonal Forest	-----
Austro-Brazilian Transitional Forest	Deciduous Seasonal Forest	Subtropical Deciduous Forest
Quebrachal of *Schinopsis balansae*	Thorn Woodland	-----
Quebrachal of 3 quebrachos	Deciduous Seasonal Forest/Thorn Woodland	Dry Subtropical Forest
Quebrachal of white quebracho	Thorn Woodland	-----
Quebrachal of 2 quebrachos	Deciduous Seasonal Forest/Thorn Woodland	Dry Subtropical Forest
Palosantales of *Bulnesia sarmientoi*	Deciduous Seasonal Forest/Thorn Woodland	-----
Arid Chaco Woodland	Thorn Woodland	Dry Subtropical Wood.
South Sierra Chaco	Deciduous Seasonal Forest/Thorn Woodland	Dry Montane Forest
North Sierra Chaco	Deciduous Seasonal Forest/Thorn Woodland	Dry Montane Forest
Algarrobales of *Prosopis* spp.	Thorn Woodland	-----
Cardonales of *Stetsonia coryne*	Cactus Scrub	-----
Palmares of *Copernicia australis*	Seasonal-Swamp Thicket with Palms	-----
Vinalares of *Prosopis ruscifolia*	Thorn Woodland	-----
'Palo blanco' forest	Deciduous Seasonal Forest	Deciduous Subtropical Forest
'Tipa' and 'Pacará' forest	Deciduous Seasonal Forest	Deciduous Subtropical Forest

2.3.2- 'Selva de ribera' (River margin forest), 'Selva' or 'Monte Alto':

This forest can be found side by side with the previous unit but on higher ground, which is never reached even by the extraordinary floods of the Paraná river (Lewis et al., 1987). In the provinces of Chaco and Santa Fe there is a strong erosion scarp 3 m high (Popolizio et al., 1980b) left by an ancient course of the river Paraguay (Popolizio, 1970), and which extends in N-S direction from the cities of Resistencia to Santa Fe and is the effective western limit of the alluvial valley of the river Paraná. It holds an up to 30 m tall forest, locally called 'selva' for its abundance in lianas and epiphytes (Schulz, 1967) and its floristic richness. It is very closely related to the previous unit, with which it is often confused, and most available descriptions have mixed floristic lists (Hauman, 1931; Ragonese, 1941; Hueck, 1972; Sarmiento, 1972; Cabrera, 1976; Reboratti & Neiff, 1986). However, the unique topographical position above the highest possible peaks of floodings, on well developed soils (typical Argiudols, Espino et al., 1983), and the peculiar floristic composition - free from hygrophilous trees such as the Lauraceae, and from inland xerophytic Chaquenian trees - allow for a definitive detachment from the Gallery Forest. To date only Schulz (1967), Morello & Adámoli (1974), and Prado et al. (in press, a) show this forest as a distinct unit; the latter provide not only a floristic list but also a quantitative assessment of this 'bosque subtropical semideciduo' dominated by *Holocalyx balansae* , *Ficus luschnathiana* and *Patagonula americana* . Again this forest is an impoverished version of floristically much richer formations in Brazil (Klein, 1967 & 1972) and Paraguay (Tortorelli, 1967). The floristic composition shown in Table 6.1 is basically the Prado et al. (op. cit.) list, with the addition of those species cited by Morello & Adámoli (1974) which appear further north because of a latitudinal enrichment of this unit.

2.3.3- Eastern Chaco Forests (sensu Morello & Adámoli, 1968, see above):

In this area there are two major woody communities which have been repeatedly mistaken for a single one (e.g.: Hauman, 1931; Ragonese, 1941; Hueck, 1959 & 1972; Ragonese & Castiglioni, 1970; Cabrera, 1971 & 1976; Sarmiento, 1972; Marlange, 1972; Cabrera & Willink, 1980; Bucher, 1982a). Although Morello & Adámoli (1974, p. 103) hint at these differences when they refer to the forestal types 'monte alto' and 'monte fuerte', it was not until Lewis & Pire (1981) pointed out their

very distinct topographical position and soil substratum that the matter was settled. These two major subunits are:

(a) Austro-Brazilian Transitional Forest:

This forest corresponds to what Lewis & Pire (1981) denominated 'bosque chaqueño', and the 'monte alto' in Morello & Adámoli (1974). It occupies the highest topographical position in NE Santa Fe, eastern Chaco administrative province and eastern Formosa (Morello et al., 1971), in well developed and intermediate soils (Ledesma, 1973; Espino et al., 1983). Usually two strata can be distinguished, the superior continuous but of variable density. Lianas and epiphytes are frequent but not abundant, and in dense stands shrubs are inconspicuous. The floristic composition suffers an evident N-S temperature gradient, and is much richer in the Chaco and Formosa provinces. The dominant species of this kind of forest are what Hauman (1931) called "elements venus des forets hygrophiles: *Tecoma ipe* , *Patagonula* , *Gleditschia* , quelques Myrtacees...". The simple-leaved 'quebracho' *Schinopsis balansae* , if at all present, is here a foreigner coming from the nearby communities of the next unit, and is usually scarce and in marginal position (Pire, E.F., unpublished data; Lewis, *in litt.*). In Table 6.1 the floristic list is shown, compiled from Lewis and Pire (1981) and the author's field experience for NE Santa Fe; further north in Argentina several other very important species are added to this community, such as *Astronium balansae* , *Diplokeleba floribunda* , *Ceiba speciosa* (Morello et al., 1971; Morello & Adámoli, 1974), or even *Pithecellobium scalare* and others (Cabrera, 1976).

(b) 'Quebrachal' (quebracho woodland) of *Schinopsis balansae* :

Also called 'monte fuerte' in Morello & Adámoli (1974), and 'quebrachal' in Lewis & Pire (1981). This unit is always found at a lower topographical position than the previous one, on heavy-textured soils of the saline cycle, such as typical Natracualf with over 15% of Na++ in the exchangeable ion complex (Espino et al., 1983). Furthermore, the ground is usually waterlogged in the rainy season because of the strongly argilic subsoil, local microrelief and consequent impeded drainage. Durland (1924) pointed out the close relationship between the Quebrachal and underground water, since it had been consistently established that water originating from subterranean sources within a belt or patch of quebracho-forest is invariably brackish, while beyond the limits of this

community it is invariably fresh (obviously out of the range of sodium-rich soils). Thus the dominant hygrophilous tree species of the Austro Brazilian forest are excluded from this kind of substratum and the forest is dominated by *Schinopsis balansae* ('quebracho colorado chaqueño'), from which this community derives its name. Two arboreal strata can be distinguished, the higher generally composed of *Schinopsis* , *Aspidosperma* and *Caesalpinia* spp., and the lower by Mimosoideae, *Schinus* and *Celtis* spp.. Often the lower stratum comprises only a dense population of young *S. balansae* treelets. The broken canopy allows a shrubby layer which is far more conspicuous than in the previous unit, and Cactaceae are a common feature. In slightly higher areas where the quebracho can generate a dense, continuous canopy, massive spiny Bromeliaceae populations predominate. Lianas and vines are extremely scarce, but the abundance of lichens and epiphytic *Tillandsia* is a typical feature of this formation. The flora listed in Table 6.1 for this forest is a compilation from Lewis & Pire (1981) and the author's field experience.

2.3.4- Central Chaco Forests:

Essentially this sector is transitional to both the Eastern and Western ones; it does not possess a floristic individuality that could characterize its vegetation. However, from an ecological point of view some of the communities to be found here are unique, or nearly so, to this sector, such as the case of the 'quebrachal of three quebrachos' unit. It is in the Central Chaco where the *Elionurus muticus* savannas are more conspicuous and have provided most of the agricultural land. These savannas are mainly determined here by heavy-textured soils with a perched water table (Beek & Bramao, 1968; Bucher, 1982a), whereas in Eastern Chaco they are determined either by strong salinity or by flooding tolerance.

(a) 'Quebrachal' of three 'quebrachos':

This unit, treated in detail by Lewis & Pire (1981), is also called 'Bosque Mixto' (Mixed Forest) in Ragonese & Castiglioni (1970). It has been briefly described in Ragonese (1941), Sarmiento (1972), Morello & Adámoli (1974) and Bucher (1982a). This unit is characterized by the shared dominance of *Schinopsis quebracho-colorado* , *Schinopsis balansae* and *Aspidosperma quebracho-blanco* . This is the only area within the Chaco in which the three species occur together in the same

community. This forest, with its definitely more xerophilous character than those in the east, consists of two continuous and dense arboreal strata (Lewis & Pire, 1981), the higher comprising the three dominants plus generally *Ziziphus mistol* , *Caesalpinia paraguariensis* and sometimes *Sideroxylon obtusifolium* . There is a conspicuous shrub layer, while the herbaceous layer is very variable in importance or absent. The floristic composition of this unit for NW Santa Fe (Lewis & Pire, 1981; also Ragonese, 1941, and personal field experience) is shown in Table 6.1.

(b) 'Quebrachal' of white 'quebracho':

Described in Lewis & Pire (1981) and D'Angelo et al. (1987) and also in Morello et al. (1971). Mainly towards the south-east of the sector, but also in localized areas elsewhere within the Central Chaco, the *Schinopsis* spp. disappear and *Aspidosperma quebracho-blanco* takes over dominance. This unit is somewhat lower, with variable density of the arboreal layer; there is a scattered emergent stratum of *A. quebracho-blanco* , from 5 to 8 m high in the south to 8 to 16 m high in the north. The bulk of the forest is in the second stratum, 4 to 5 m high in the south and up to 8 m in northern areas. In the Formosa province this community can be found on slightly elevated areas above the position of the 'vinalares' (see) on less alkaline loamy soils (Morello et al., 1971). The floristic composition shown in Table 6.1 has been compiled from Lewis & Pire (1981) and Morello et al. (1971).

2.3.5- Western Chaco Forests:

In this part of the region environmental factors such as rainfall are more uniform (Table 2.1), and consequently the vegetation is more homogeneous. Western Chaco is the driest, most continental sector, with the highest maxima and lowest minima in both absolute and average temperature values, longest frost period, and its vegetation shows the most pronounced xeromorphy. Cactaceae are very abundant here, and amongst them the arborescent habit is particularly conspicuous: *Stetsonia coryne* , *Opuntia quimilo* , *Cereus validus* , *Quiabentia pflanzii* , *Pereskia sacharosa* . Lianas and epiphytes are generally extremely rare. There are a number of anthropogenic communities (Morello & Saravia Toledo, 1959a & b), because of both the higher fragility of these semiarid ecosystems and older european colonization. A few endemic genera (*Lophocarpinia* , *Mimoziganthus* ,

Stenodrepanum , *Setiechinopsis*) are present as well as numerous endemic species (Ragonese & Castiglioni, 1970) and there is also an important intrusion of species coming from the Monte phytogeographical province (Morello, 1958).

(a) 'Quebrachal' of two 'quebrachos':

This unit of Adámoli et al. (1972) it is also known as 'quebrachal of quebracho-colorado' (Ragonese & Castiglioni, 1970), plain 'quebrachal' by Morello & Adámoli (1968), forests of quebracho colorado and quebracho blanco in Cabrera (1971, 1976), 'quebrachaie' in Marlange (1972). Also described briefly in Castellanos (1958), Hueck (1959, 1972), Sarmiento (1972), Bucher (1982a), and extensively in Morello & Saravia Toledo (1959a & b) and Morello & Adámoli (1974). It consists of a medium-tall forest, 16-18 m high, with a second arboreal stratum 12 m high, and it is the most widespread vegetation unit in this sector. The area dominated by this kind of forest coincides roughly with Ragonese & Castiglioni (1970) 'Santiaguenian District' in their Western Chaco Park, excluding the subdistrict 'Santiaguenian Park' which corresponds to the Central Chaco. It also matches well with the 'Woody Chaco' of Morello & Adámoli (1968). There are other minor communities within the range of this forest, such as the 'iscayantales' of *Mimoziganthus carinatus* and also communities of *Tabebuia nodosa* in depressed localities, which will not be dealt with here. The floristic composition, compiled from Morello & Adámoli (1968) and Adámoli et al. (1972) and the author's experience in the area, is shown in Table 6.1.

(b) 'Palosantales' of *Bulnesia sarmientoi* :

Studied by Morello & Adámoli (1968, 1974), Ragonese & Castiglioni (1970), Hueck (1972), Adámoli et al. (1972), and as 'forests of quebracho colorado and palo santo' in Cabrera, 1971 & 1976. The dominant species, up to 20 m high, is often accompanied by *Schinopsis quebracho-colorado* as a subdominant (Castellanos, 1958) unless the community is on clayish, heavy-textured soils with very impeded drainage and temporary anaerobiosis (Adámoli et al., 1972). The area covered by this unit, with or without the quebracho colorado, is what Ragonese & Castiglioni called the 'Matacoan District', to which some exclusive species pertain: *Jatropha matacensis* , *Lophocarpinia aculeatifolia* . The floristic composition shown in Table 6.1 is taken from Morello et al. (1971), and Adámoli et al. (1972).

(c) Arid Chaco Woodland:

Also called 'Quebrachales' of *Aspidosperma quebracho-blanco* in Ragonese & Castiglioni (1970) and Sayago (1969). This community appears everywhere within Western Chaco, particularly as a result of overgrazing pressure and selective felling (Morello & Saravia Toledo, 1959a & b), but in the SW of this area it is particularly dominant due to the disappearance here of *Schinopsis quebracho-colorado* . The latter sector corresponds to the 'Llanos District' of Ragonese & Castiglioni (1970) and also to the Arid Chaco Woodland of Sarmiento (1972). Some authors have proposed that this district should be referred to the Monte province on account of the high number of Monte intruders, but both Ragonese (1951) and Morello (1958) have demonstrated the propriety of keeping it within the Chaco. This formation shows an open and scattered arboreal stratum comprising isolated individuals of *Aspidosperma quebracho-blanco* , accompanied by mainly Chaco elements but also some Monte species, as shown by Sayago (1969, p.159) floristic list (Table 6.1).

2.3.6- Sierra Chaco:

(a) South Sierra Chaco (Pampean Sierra Chaco):

In the western fringe of the region the vegetation covering the mountainous ranges of the Pampean Sierras has been considered to be of undoubted chaquenian linage and physiognomy, despite a number of endemic species in the dominant and subsidiary taxa. The Pampean Sierra Chaco received detailed study by Sayago (1969) and Luti et al. (1979), but further analysis or mapping can be found in Morello & Adámoli (1968), Ragonese & Castiglioni (1970), Cabrera (1971, 1976), Marlange (1972), Sarmiento (1972), Bucher (1982a) and Vargas Gil & Vorano (1988). However, it was inexplicably overlooked by Hueck (1959, 1972) and Hueck & Seibert (1981) although these authors do recognize a very similar formation further north in the Subandean Sierras. Lewis, J.P. (unpublished data) distinguishes three basically different kinds of woody associations within the Pampean Sierra Chaco: a) piedmont Sierra forest, mainly comprising *Prosopis* spp.; b) 'quebrachal' of *Schinopsis haenkeana* in middle slope; c) 'mollar' of *Lithraea ternifolia* on the slopes above the quebrachal and below the shrublands of *Flourensia* or *Heterothalamus* spp., and also in the south of this sector where *S. haenkeana* disappears (Lewis & Pire, 1981). The floristic list of

what Sayago (1969) qualified as the most typical Sierra Chaco forest is included in Table 6.1.

(b) North Sierra Chaco (Subandean Sierra Chaco):

A rather more contentious issue is raised by the entity referred to as the Subandean Sierra Chaco. Some authors have apparently merged this unit with the so-called Transitional Forest (Morello & Adámoli, 1968; Ragonese & Castiglioni, 1970), whereas others (Hueck, 1959 & 1972; Cabrera, 1971 & 1976; Marlange, 1972; Adámoli et al., 1972; Sarmiento, 1972) have separated them, a treatment favoured here since floristic composition clearly links the Subandean to the Pampean Sierra Chaco (cf. Marlange, 1972, list for the Lomas de Olmedo area in Table 6.1). Because it only occupies a small area and interdigitates with the several neighbouring phytogeographical provinces, this forest has been generally omitted from vegetation maps with the exception of Vervoorst's detailed regional map in Hawkes & Hjerting (1969, p. 38).

2.3.7- Azonal woody formations of the Chaco:

(a) 'Algarrobales' - *Prosopis* spp. communities:

These thorn woodlands, also called 'raleras' (Morello & Adámoli, 1974), are found throughout the Chaco proper in low lying areas. In E Chaco, if the topographic gradient is followed down from the *Schinopsis balansae* 'quebrachales' towards a high water table, the first species to disappear is *S. balansae,* followed by *Caesalpinia paraguariensis* and most of the accompanying species of the 'quebrachal', until the arboreal stratum is reduced to mainly *Prosopis nigra* or *P. alba* dominated stands. These 'algarrobales' are common around seasonal swamps or small, somewhat undefined streams; the soil is regularly flooded in the rainy season mostly by overflow from the adjacent water courses. When the flooding recedes, the salinization process of soils is resumed, resulting generally in typical Natracualf or Natracuol (Espino et al., 1983). The arboreal stratum may be very simple: *P. nigra, Geoffroea decorticans, Aspidosperma quebracho-blanco* and *Acacia caven* , and is continuous and often dense and just over 3 m high (Lewis & Pire, 1981). There is no well defined shrub layer, and during the dry season the herbaceous layer has very low coverage or is absent altogether. Further north in the Formosa province (Morello et al., 1971) the 'algarrobales' show a much richer composition as shown in Table 6.1.

(b) 'Cardonales' of *Stetsonia coryne* :

This kind of low-height formation is scarce in Eastern Chaco (Lewis & Pire, 1981), but much more frequent in Western Chaco (Sayago, 1969). It is dominated by candelabra-like individuals of the monotypic Cactaceous genus *Stetsonia* , endemic to the Chaco, and usually 60% or more of the strongly saline soil is bare ground or it is covered only by mosses and *Selaginella sellowii* . The stands are very poor in the east, but a much richer western one is listed in Table 6.1 from Sayago (1969). Similar communities are described by Adámoli et al. (1972), and *sub* 'peladares' by Ramella & Spichiger (1989) for Paraguay.

(c) 'Palmares' of *Copernicia alba* :

These palm groves and savannas usually comprise a nearly monospecific open arboreal layer of very variable density, 8 to 10 m high, of this fan-leaved palm-tree. They are always found in low lying position close to or within marshes, on seasonally flooded alkaline soils (Ragonese, 1941; Ragonese & Castiglioni, 1970). The herbaceous layer is dominated by *Spartina argentinensis*, though sometimes *Paspalum* spp. might replace it (Lewis & Pire, 1981). Additional information can be found in Markley (1955), Hueck (1959, 1972) and Dahlgren & Glassman (1961); references for Paraguay in Fiebrig (1933), Rojas & Carabia (1945), Tortorelli (1967), Esser (1982), Spichiger & Ramella (1989) and Ramella & Spichiger (1989). Citations of this community in the Bolivian Chaco in Werding (1976), and for Brazil in Veloso (1947), Prance & Schaller (1982) and Ratter et al. (1988b). The more complete floristic lists of these 'palmares' available to date refer to the Argentine Chaco, such as those in Cabrera (1976) and Lewis & Pire (1981) for the Eastern Chaco shown in Table 6.1, together with the author's field experience; the 'palmares' in Western Chaco show a somewhat different composition (Morello & Saravia Toledo, 1959a; Cabrera, 1971, 1976; Adámoli et al., 1972), and it is also provided in Table 6.1.

(d) 'Vinalares' of *Prosopis ruscifolia* :

In Central and Western Chaco the areas under the influence of the only three rivers running across the Gran Chaco are ecologically very unstable; the lack of energy of these flat plains generates a wide divagation of the water courses, and subsequently creates new open spaces to be colonized, especially alkaline swamps in dessication (such as

drying-out abandoned ox-bows). *Prosopis ruscifolia* is particularly adapted to this kind of environment and successfully colonizes large expanses of land, even forming virtually monospecific communities with no herbaceous layer and where the shrub stratum is the only one to add some variability. There is a host of different facies for these woodlands according to relative degrees of flooding, salinity or anthropogenic influence, as studied proficiently and extensively by Morello et al. (1971). In Table 6.1 the floristic composition of a typical 'vinalar' is provided.

2.3.8- Subandean Piedmont Forests (usually known as Transitional Forests):

These forests occupy a narrow strip between the dry forests of Western Chaco and the more humid Lower Montane Forest (Sarmiento, 1972) or 'Distrito de las Selvas Montanas' (Cabrera, 1976), extending in a meridional fashion from the area of Santa Cruz de la Sierra in Bolivia to slightly south of the limit Tucumán-Catamarca provinces in NW Argentina. Their very peculiar position as a wedge between two major phytogeographical units (the Chaco and Yungas provinces, *sensu* Cabrera, 1976), at an intermediate altitude (350 to 500 m in Cabrera, 1976, or 450 to 900 m in Meyer, 1963), and also with intermediate rainfall figures (from 700 to 1000 mm) of monsoonian character (Vervoorst, 1982), allows for a particular kind of forest to develop with its own floristic identity. According to Sarmiento (1972) this formation has the highest proportion of deciduous species (79 %) of all the subtropical seasonal forests. They are located in the piedmont area of the Subandean Mountains in SW Bolivia and NW Argentina (hence their name), but their southernmost extension is actually placed in the northern extreme of the Sierras Pampeanas in S Tucumán and E Catamarca.

Towards the east and down the topographic gradient these forests intermingle with Sierra or Western Chaco, whereas to the west and uphill they receive some elements from the Yungas forests. Some authors have regarded the Transitional Forests as having more in common with the Chaco area than with the Yungas (Hueck, 1959 & 1972; Morello & Adámoli, 1968; Ragonese & Castiglioni, 1970; Marlange, 1972; Hueck & Seibert, 1981; Vargas Gil & Vorano, 1988). However, leaving aside the negligible ecotonal areas with Chaco proper, their floristic composition clearly puts them within the Yungas or Tucumanian-Bolivian Forests province (Hauman, 1931; Meyer, 1963; Cabrera, 1971,

1976). Correa Luna (1955) describes a locality in which Piedmont Forest occurs side by side with Chaco scrubland, but their elements do not intermix at all: at this site there is a relatively dry valley, the lower plains of which are covered by *Acacia* spp., *Prosopis* spp., *Geoffroea decorticans* , *Celtis spinosa* , *Opuntia* sp. and *Cereus* sp., while small elevations within the range of this valley hold *Anadenanthera colubrina* var. *cebil* , *Pterogyne nitens* , *Ceiba chodatii* , all species which can also appear in the tall humid forests on the nearby mountains bordering the valley. Species of the genera *Schinopsis* , *Caesalpinia* , *Cercidium* do not appear in the valley, since they belong to less elevated grounds (i.e. the Chaco plains).

There are two major types of forests within this unit, ordered in N-S direction by a temperature gradient, and separated by a gap dividing the mountainous ranges (Vervoorst, in Hawkes & Hjerting, 1969, p.38) which allows the intrusion of Chaco communities into the inner dry valleys (e.g. the Lerma valley):

(a) 'Palo blanco' forest:

This unit takes its name from its most conspicuous dominant, the elegant Rubiaceous tree *Calycophyllum multiflorum*. Also known as 'Übergangswalder' in Kanter, 1936; 'Forest with *Calycophyllum multiflorum*' in Hueck, 1954, 1959 & 1972; 'High Mesophytic Forest' in Coro, 1956; 'Palo blanco and Palo amarillo' forest in Cabrera, 1971 & 1976; 'Paloblancal' in Sarmiento, 1972; 'Bosque Húmedo Templado' in Unzueta, 1975 (p. 218). It was briefly studied by Frenguelli & Cabrera (1938), Meyer (1944), Adámoli et al.(1972) and Marlange (1972), and mapped by Hueck (1954), Vervoorst (in Hawkes & Hjerting, op.cit.), Unzueta (1975), Hueck & Seibert (1981), and Vargas Gil & Vorano (1988). Unfortunately, and despite the apparent wealth of references, this forest is one of the least known vegetation units in Argentina, a fact also pointed out by Unzueta (1975, p.223) for Bolivia. Placed on good agricultural soils, and located along the corridor of the early Spanish colonization, it was cleared or well-logged before any settlement was established in, for example, neighbouring Chaco forests. The present day information on this forest is therefore extremely scanty and patchy, and although some relictual stands seem to remain in NW Argentina and in Bolivia, a thorough phytosociological study has never been carried out.

In NW Argentina this unit reaches 30 m high, with white straight boles up to 1 m diameter mainly of 'palo blanco' (*Calycophyllum multiflorum*) and 'palo amarillo' (*Phyllostylon rhamnoides*). A shrub layer of about 2 m high makes transit very difficult, together with abundant lianas, vines and epiphytes (Cabrera, 1976), which are completely absent from the nearby dry Chaco forests. The floristic list of Table 6.1 has been compiled from Meyer (1944), Coro (1956), Adámoli et al. (1972), and Cabrera (1976).

(b) 'Tipa' and 'Pacará' forest:

This is a latitudinally impoverished version of the previous unit, deprived of the two major dominants ('palo blanco' and 'palo amarillo'). It underwent a complete destruction by human activity, as pointed out by Hauman in 1931, and nowadays sugar cane fields and citrus orchards are found instead. Paradoxically the 'tipa' (*Tipuana tipu*) and 'pacará' (*Enterolobium contortisiliquum*) forest is somewhat better known than the previous unit, with brief descriptions to be found in Hauman (1931), Hueck (1954, 1959, 1972), Meyer (1963), Digilio & Legname (1966) and Cabrera (1971, 1976). A complete phytosociological survey of a stand, itself transitional between these two subunits, was performed by Brown et al (1985) *sub* 'selva de quina y cebil'. Its floristic composition is shown in Table 6.1, compiled from some of the aforementioned references.

2.3.9- The Brazilian Chaco problem:

A number of phytogeographical accounts and vegetation maps of South America depict a narrow wedge of so-called Chaco vegetation, entering into Brazil in SW Mato Grosso do Sul state as a continuation of the main area in Argentina, Paraguay and Bolivia (Fig. 1.1). The alleged presence of Chaco forests in that area has been reported by diverse authors, e.g. Hueck (1955, 1959, 1972), Morello & Adámoli (1968), Ragonese & Castiglioni (1970), Cabrera & Willink (1980), Hueck & Seibert (1981), Bucher (1982a), Prance & Schaller (1982), Adámoli (1982), Eiten (1983), Ratter (1984), Allem & Valls (1987), and Ratter et al. (1988b). The first phytogeographer to report 'bosques chaquenhos' within Brazil was Hueck (1955), and he included a map showing the extent of the Chaco intrusion in Mato Grosso, which has been followed by all subsequent workers. However, Prado et al. (in press, b) carried out a survey in the spur of Chaco in Brazil in 1989, on the basis of which they segregated the

vegetation into five major woody communities: a) *Diplokeleba -Tabebuia - Capparis* scrubland; b) *Schinopsis balansae* parkland; c) *Aspidosperma - Mimosa* scrubland; d) Calcareous woodland; e) Chaquenian forest at Porto Murtinho (see Table 6.1 for their floristic composition).

The latter community is the only one they accept as truly chaquenian, with about 70% of Chaco elements *s.s.* between both dominant and accompanying species. The first three communities are regarded as transitional, since they comprise only a minority of chaquenian elements together with cerrado and semideciduous forest species. Finally, the *Schinopsis brasiliensis* -dominated calcareous woodlands are absolutely non-chaquenian, both in physiognomy and floristic composition, and some of its elements can be found elsewhere in South America in formations such as the Caatingas in NE Brazil, the Yungas of Bolivia and Argentina (particularly in the so-called Transitional forests), and the subtropical forests on both banks of the rivers Paraguay and Paraná (Prado et al., in press, b). No trace was found in the studied area of *Schinopsis quebracho-colorado* , although this should be a very frequent and dominant tree according to Hueck (1955), and these authors conclude that a case of mistaken identity with *S. brasiliensis* misled Hueck. Thus, the extent of the Chaco ingression into Brazil, which is a meeting place for three different floristic stocks, is dramatically diminished, now restricted to a reduced area around Porto Murtinho, far less than previously thought and hardly mappable on a continental scale.

Plate 2.1: Some aspects of the Chaco vegetation. Top: scrub dominated by Mimosoideae in Quimilí, Santiago del Estero, Arg. Center: *Elionurus muticus* savanna in NW Santa Fe, Arg. Bottom: *Schinopsis quebracho-colorado* forest in Quimilí.

3. THE CAATINGAS VEGETATION

The Caatingas province in NE Brazil extends from 2º 54' S to 17º 21' S (*ca* . 850,000 km^2), and includes the states of Ceará, Rio Grande do Norte, most of Paraíba and Pernambuco, SE Piauí, W Alagoas and Sergipe, north and central Bahia, and a wedge extending into Minas Gerais following the São Francisco river together with an outpost in the dry valley of Middle Jequitinhonha river (Fig. 1.1). Fernando de Noronha island should also be included (Andrade-Lima, 1981). The name 'caatinga' is of Tupí-Guaraní amerindian origin and is usually taken to mean 'white forest'[1], which certainly well characterizes the aspect of the vegetation in the dry season, when all leaves have been shed and only the bright white trunks of trees and shrubs are left in a desiccated landscape. Martius referred to the Caatingas as *Hamadryades* or the descriptive phrases '*silva horrida* ' or '*silva aestu aphylla* ', the latter ('the forest leafless in summer') following local custom in treating the rainy season of the Caatingas as 'winter', although it actually coincides with the summer solstice.

Unfortunately, the name 'caatinga' has also been widely used for the geographical region of NE Brazil, and this has given rise to some confusion, as with the similar use of the word 'Chaco' (Castellanos, 1960). The concept of the Caatinga Region includes areas such as the Chapada do Araripe, with cerrado vegetation, or the wetter sectors of the 'brejos' of Pernambuco, with rain or cloud forests, and excludes areas which, although floristically part of the Caatingas vegetation, are not considered to be in the geographical region, such as the dry valley of the Jequitinhonha river in Minas Gerais or certain parts of the Rio Grande basin in W Bahia. It should also be emphasized that the phytogeographical concept of the Caatingas used here does not include Amazon Caatingas, which are a floristically unrelated kind of white-trunked forests restricted to extremely dystrophic white sands in the Amazon region. Following Andrade-Lima (1966a) it is accepted that the province should be called 'the Caatingas', in plural, since it includes several different physiognomies of vegetation and numerous facies,

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[1] The Tupí-Guaraní etymology consists of the particles ca'a, plant or forest; tî, white (derived from morotî, white); and the suffix 'ngá (from angá), resembling, near to (Peralta & Osuna, 1952). Thus, "the whitish forest".

which are generally referred to as 'caatinga' plus either a vernacular or technical epithet (e.g. arboreal caatinga).

3.1- Geology and geomorphology of the Caatingas:

In the Brazilian northeast most of the Caatingas vegetation areas are located on intertableland depressions (Ab' Sáber, 1974, *sub* 'depressões interplanálticas'), but some localized exceptions occur, such as the low 'chapada' (tableland) of Raso da Catarina (Bahia), the Borborema range in Paraíba, or the Apodi plateau in Rio Grande do Norte where Caatingas vegetation is found not only in the depressions but also on the highlands (Andrade-Lima, 1981). In the main, however, this province extends over undulated pediplains (Andrade & Lins, 1965, p.21), dissected from Cretaceous or Tertiary sediments covering the underlying Pre-Cambrian Brazilian Shield (Cole, 1960). A massive process of pediplanation took place during the late Tertiary and lower Quaternary (Ab' Sáber, 1974) to uncover the present-day surface of Pre-Cambrian crystalline rocks (gneiss, granites and schists), and leaving only isolated relics of the younger surfaces scattered throughout the Caatingas. These remnants are referred to as inselbergs (such as those in Quixadá - Ceará, and Patos - Paraíba), 'serras', or 'chapadas', in order of decreasing erosion. Thus, the 'chapadas' usually still show the complete features of the original Tertiary sedimentary sandstone surfaces, whilst the 'serras' indicate a more advanced stage of the process of pediplanation and the inselbergs are the last remains yet to be eroded away. In general their vegetation varies accordingly, with cerrado vegetation on top of the Tablelands (such as the Chapada de Araripe and the coastal 'taboleiros'), semideciduous or evergreen wet forests on top of the 'serras' (such as the 'brejos' of Pernambuco; see Andrade-Lima, 1964b, and Andrade & Lins, 1964), and dry forests or arboreal caatinga formations on the slopes and on the inselbergs (Fig. 3.1, modified from Cole, 1960). There are also some sedimentary areas within the Caatingas, such as those in Rio Grande do Norte - coastal areas and the river Mossoró basin (Andrade-Lima, 1964c), and in Bahia the Raso da Catarina and sectors under the influence of the São Francisco river.

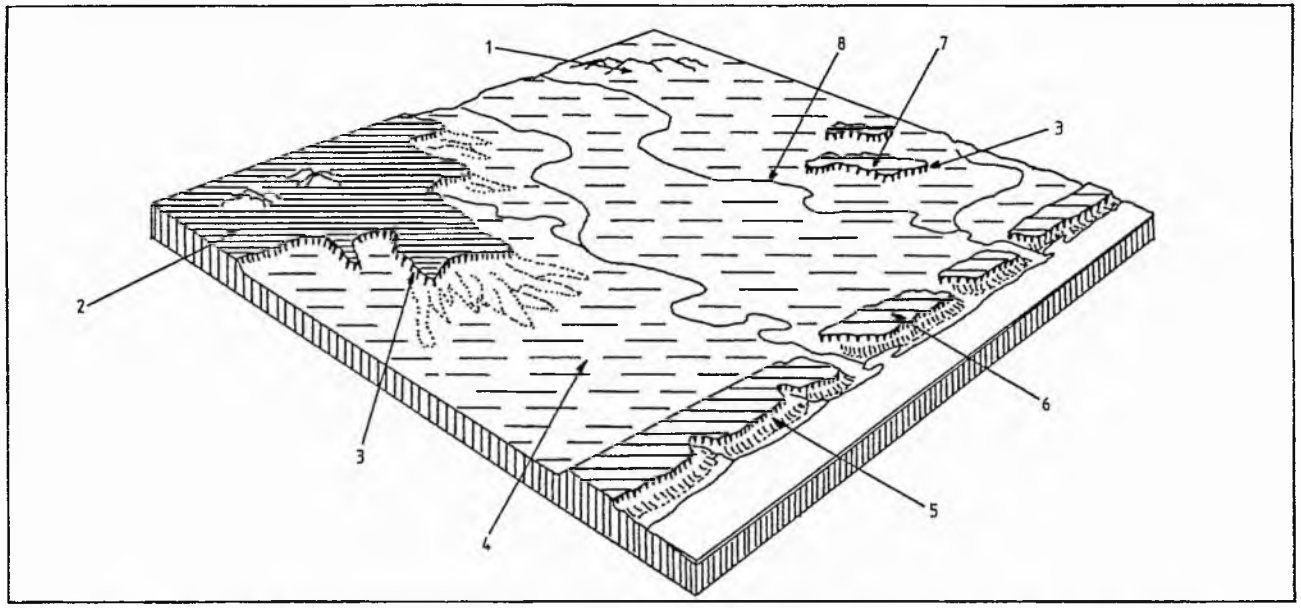

Fig. 3.1: Relationship between vegetation and geomorphology in NE Brazil (redrawn from Cole, 1960). 1: caatinga forest on slopes of serras; 2: cerrados on Sul-Americana surface; 3: caatinga forest or dry forest on escarpment slopes; 4: caatinga scrub on Paraguaçu surface; 5: rainforest covering dissected terrain of coastal zone; 6: cerrado on coastal taboleiros; 7: cerrado on remnants of Velhas surface; 8: forests following stream courses.

As a result of this genesis of the Caatingas substratum the soils are stony and shallow, with a scarcely decomposed bedrock at about 1 m deep, and very frequent massive rock outcroppings (Tricart, 1961; Ab' Sáber, 1974). The slightly undulated, hilly country so characteristic of the 'sertão', has originated in the process of pediplanation following two main types of erosive processes (Tricart, 1961): millimetric exfoliation, peculiar to this province and only some millimetres deep which results in abundant sand taken away by run-off waters to the foot of the pediments, fashioning the inclined plains typical of the topography of the semi-arid NE Brazil; and metric exfoliation, about 1 m deep and exploring fissures parallel to the surface, yielding large boulders found at the foot of inselbergs and crystalline mounds.

The morphogenetical action of run-off water takes three main forms in the Caatingas (Tricart, 1961): a) in crystalline hills with abundant naked rock there is an immediate quick drainage of rainfall, with scarcely any mechanical effect but mostly chemical corrosion; b) diffuse drainage along the pediments, the run-off water carrying away the finest particles (clay, silt, fine sand) and leaving behind coarse sand, gravel and stones to conform the characteristic extensive detrital pavements ; c) concentration of run-off waters downstream of the inclined plains, where they join to cut small valleys with temporary drainage. The hydrography of the region consists of seasonal intermittent watercourses with exorheic drainage (Ab' Sáber, 1974); in drier years the rivers in the affected sectors become sporadic or ephemeral. Such rivers flow during the rainy season, but gradually disappear subsequently, and during this annual terminal phase the rivers seem to receive a residual feeding from the, at the time, full water table; no sooner have the rains ceased than a hydrological inversion takes place, this phenomenon being responsible for the disappearance of the watercourses: the river feeds back to the water table and dries away until the next rainy season.

It has been postulated that during the Quaternary the Caatingas did not undergo the marked climatic changes which affected other areas of Brazil (Cailleux & Tricart, 1959). The only evidence of a Pleistocenic fluctuation has been provided by certain localized layers of rough pebbles which seem to be the product of a more torrential regime.

However, evidence accumulated recently indicates that NE Brazil had an even drier climate during certain periods of the Quaternary, originating the palæodune fields of Xique-Xique, Bahia (Ab' Sáber, 1977a; Tricart, 1985). These æolian formations must have originated when the aloctonous São Francisco river, the only major perennial river to cross the Caatingas, dried up in its middle course (probably close to the locality of Barra, Bahia) and the sandy and loamy alluvial sediments previously spread in the area were shaped into dunes by mainly easterly winds (Tricart, 1985). It is supposed that the middle São Francisco and its tributaries are presently at a climatic limit of exorheism, and that any serious and permanent fall in precipitation will result in endorheic conditions (Tricart, 1985) with subsequent increase in salinity.

3.2- Climate:

The semiarid Caatingas, compared to other Brazilian formations, hold most of the extreme values amongst the meteorological parameters: highest solar radiation, lowest cloudiness, highest annual average temperature, lowest percentages of relative humidity, highest potential evapotranspiration, and above all the lowest and most irregular precipitations, limited in most of the area to a very short period of the year (Reis, 1976). Catastrophic phenomena are very frequent, namely droughts and floodings, which have undoubtedly shaped the peculiar plant and animal life of the Caatingas. However, it is the scarcity or complete absence of rainfall in some years which mostly characterizes the region, rather than the rare local occurrence of double or even triple level of precipitation (Nimer, 1972). In an attempt to coordinate the study of the cyclic droughts successive laws have been passed by the Brazilian government to delimit the so-called 'Polygon of Droughts' (Polígono das Secas), which now roughly coincides with the phytogeographical province of the Caatingas (Fig. 3.2).

The semiarid nature of this area results mainly from the predominance of stable air masses pushed from the SE quadrant by the Trade Winds, which have their origin in the the action of the South Atlantic Anticyclone. The entire eastern coastal Brazil consists of a narrow strip of lowlands behind which there is a range of mountains extending from Rio Grande do Norte to Rio Grande do Sul: the Serra do Mar. When the water-vapour laden Atlantic Equatorial air masses are

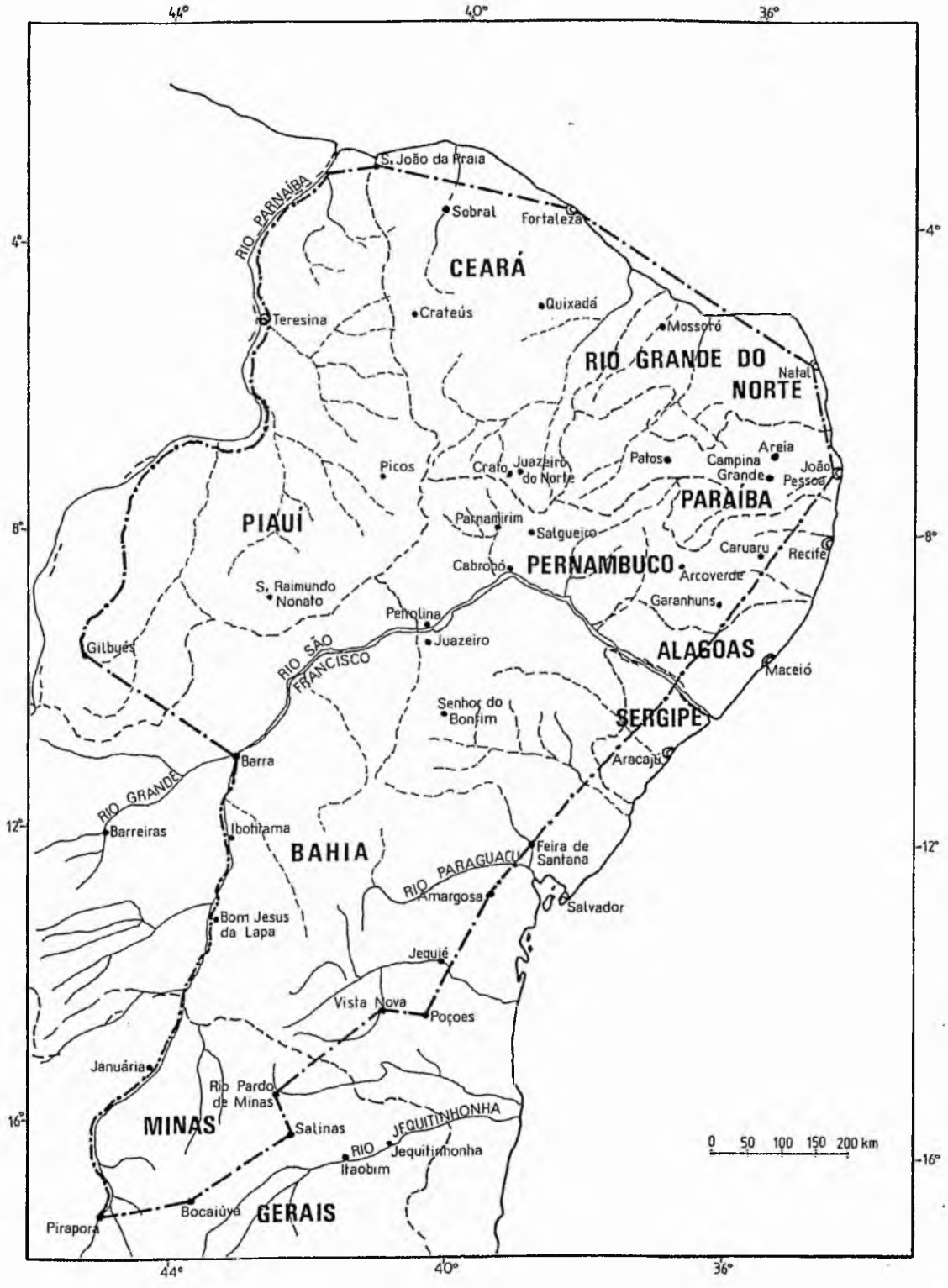

Fig. 3.2: The 'Polygon of Droughts' of NE Brazil. Redrawn from Andrade-Lima, 1981.

carried by the Trade Winds against the coastal ranges in NE Brazil, they are adiabatically cooled and precipitate annually *ca* . 2000 mm of rainfall. This is the area of the Coastal Atlantic rainforests, where the Atlantic Equatorial System loses most of its humidity, while on the rain-shadow of the mountain ranges the Caatingas lie under the effect of dry, stable air masses (Andrade & Lins, 1965). It is only when the latter encounter some of the few elevations left behind by the pediplanation process that the 'brejos' phenomenon takes place as humid islands within a semiarid region (Andrade-Lima, 1964b; Andrade & Lins, 1964), since again the air mass is raised and cooled, and deposits there its remaining water. The low pressure zone known as Intertropical Convergence or Intertropical Front, where Trade Winds of both hemispheres meet, lies roughly parallel to the Equator at about 10º N. During summer this line of encounter moves south of the Equator, bringing high instability to the weather of the northern half of the Caatingas from February to April, which is the rainy season for most of NE Brazil. The Continental Equatorial humid mass originates over Amazonia, producing there very heavy convective showers, and it can reach W Caatingas from November to January particularly when allied to the southward displacement of the Intertropical Convergence. Thus, the rainy season follows a sequence from November to January in the west and southwest, to February to April in the north and northeast, depending on the penetrations of two unstable humid masses coming from the north and west, and on their ability to displace a stable, dry mass brought in by the Trade Winds. Catastrophic droughts happen when the former are unable to reach the Caatingas because of the latter (Andrade & Lins, 1965; Reis, 1976).

It has been shown elsewhere (Nimer, 1972; Reis, 1976; Andrade-Lima, 1981) that the generally accepted phytogeographical concept of the Caatingas coincides roughly with the 1000 mm rainfall isohyets (Fig. 3.3). About 50 % of the area receives less than 750 mm, while certain localized sectors have under 500 mm, such as the Raso da Catarina, together with much of central Pernambuco and central Paraíba (Fig. 3.3). However, it is not the total amount of yearly rainfall that matters most, but rather the yearly distribution and deviation of the mode. Figure 3.4 shows that nearly all of the area under study suffers a concentration of 50 to 70 % of rainfall in three consecutives months, thus constituting a very strong seasonal climate. Throughout the area the

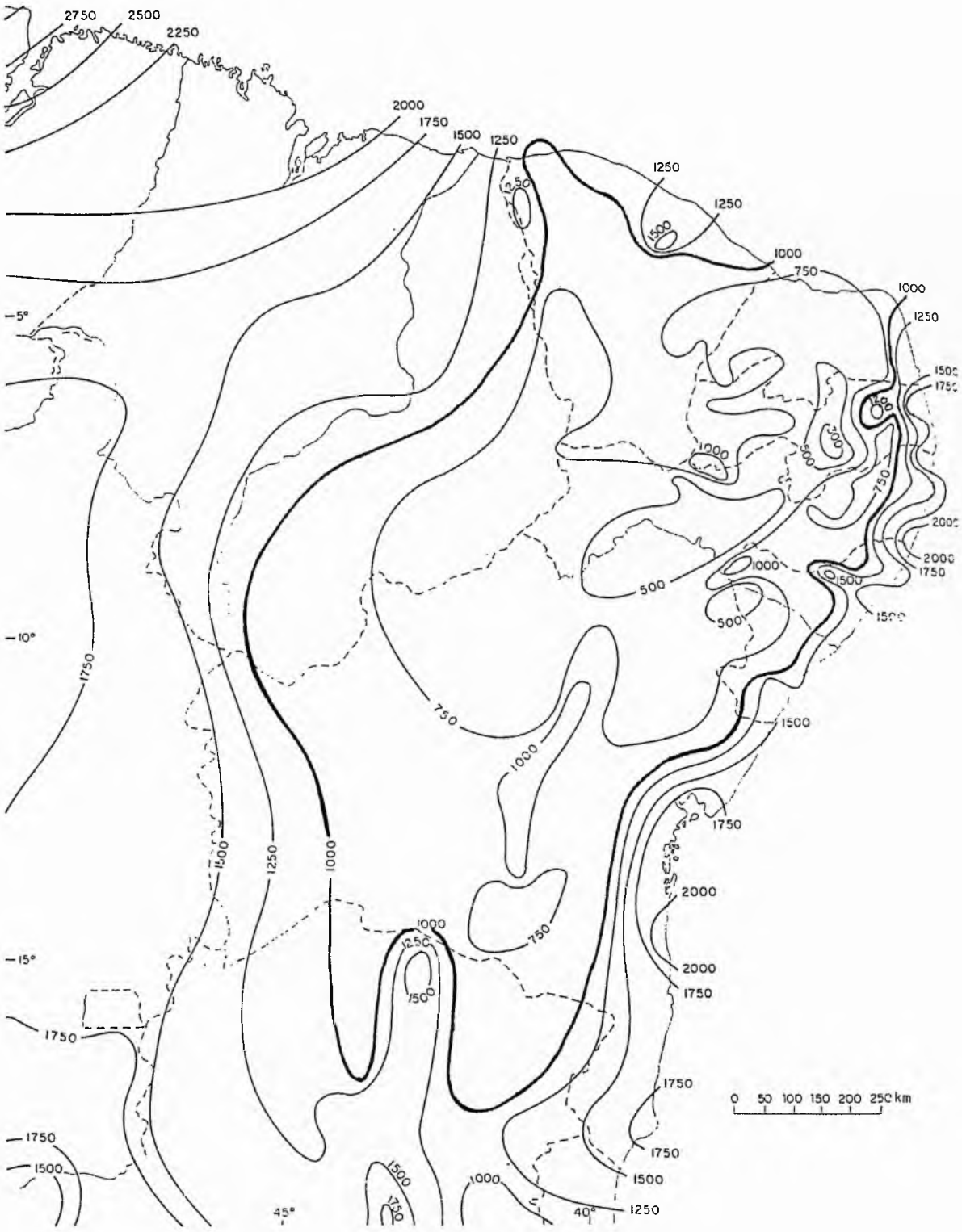

Fig. 3.3: Rainfall isolines for NE Brazil (1000 mm isohyet highlighted). Modified from Nimer, 1972.

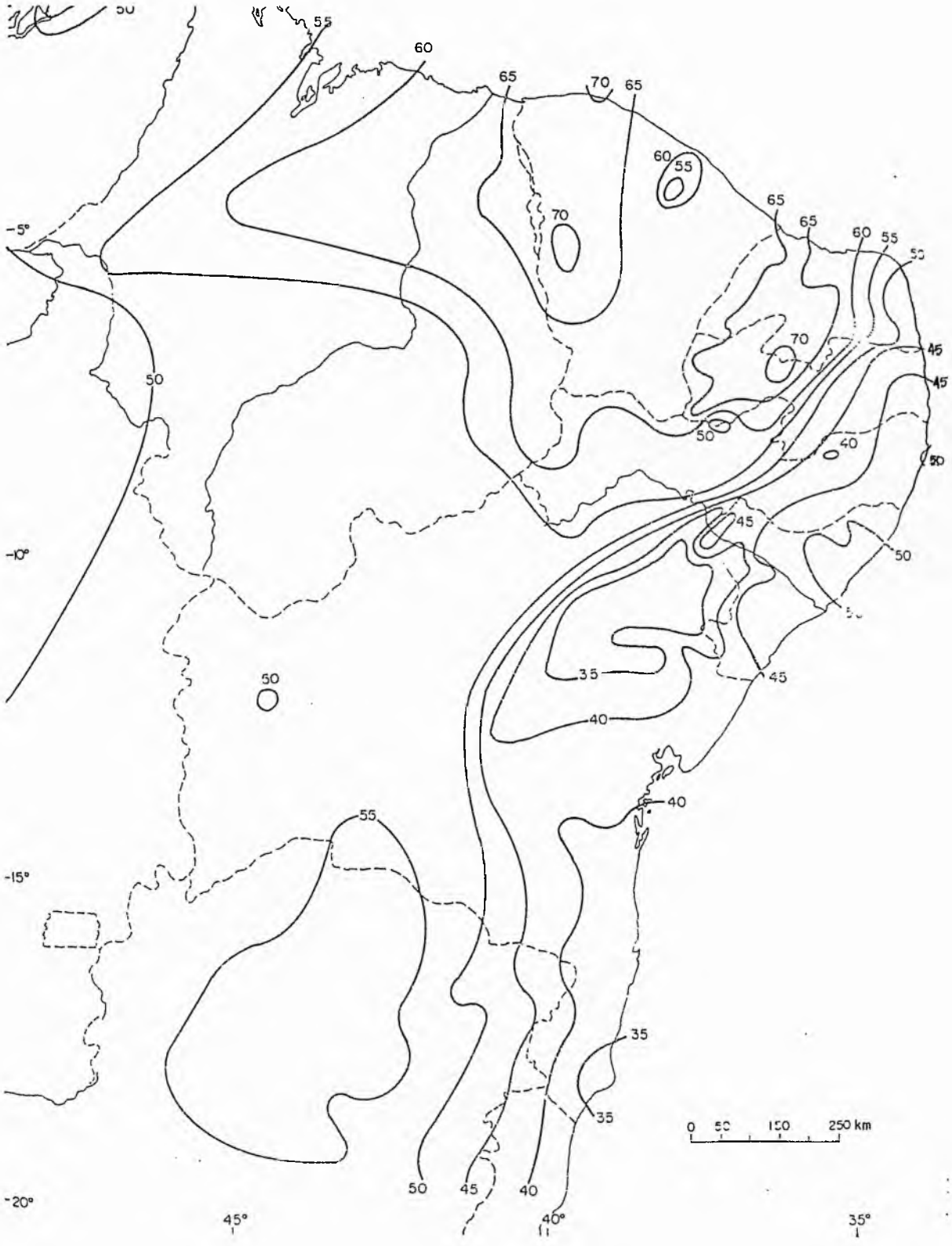

Fig. 3.4: Percentage of rainfall concentration in three consecutive months in NE Brazil. Modified from Nimer, 1972.

length of the dry season is very variable, ranging from two to three months in wet 'brejos', through six to nine months in most of the region, and up to 10-11 months in Raso da Catarina (Nimer, 1972). In general the dry period increases from the periphery to the center of the 'sertão' (Nimer, 1972; Nishizawa, 1976). The most characteristic feature of this climate is the extreme irregularity of rainfall from year to year such that the average yearly deviation expressed as a percentage ranges from 20 - >50 % (Fig. 3.5). Furthermore, those sectors with higher rainfall deviations are linked in general to those with a lower yearly total, with higher concentration in three months and consequent longer dry period (Nimer, 1972). However, since this deviation is an average figure, it does not show how marked is the irregularity. Thus, in Table 3.1, rainfall figures for Sobral, Ceará, during the period 1934-52 show an extraordinary range from 363 to 1348 mm (data from Guerra, 1955).

No frosts have ever been registered in the Caatingas, and the lowest temperatures (4°C) within the region occur as an effect of altitude in some 'serras' (Fig. 3.6). On the other hand, the average absolute maxima are rarely over 40°C (Fig. 3.7), and they are mainly restricted to the driest sectors (lower São Francisco river, and the Jequitinhonha river valley in Minas Gerais), whilst in wetter areas outwith the Caatingas such as Pará or Goiás states temperatures over 40 or 42°C are far more frequent (Nimer, 1972). However, very high mean annual temperatures are another characteristic feature of the 'sertão' (Reis, 1976), with values ranging between 26 and 28°C (Nimer, 1972), although all areas over 250 m of altitude have lower mean temperatures (20 - 22°C).

3.3- Soils:

In Section 3.1 the morphogenetical factors which give rise to the present soils of the Caatingas were explained with regard to parent material (crystalline Pre-Cambrian rocks and localized sedimentary sectors). The rock surfaces that must generate the subsequent soils under weathering action are alkaline, but rainfall water produces a dissolution of the bases which are leached away and then an acidic microenvironment is created. The formation of clays starts in weathering rock, but the prevailing pH (due to the presence or absence of bases) will determine its nature; in acidic environment kaolinite is formed, while montmorillonite will predominate if rainfall is insufficient

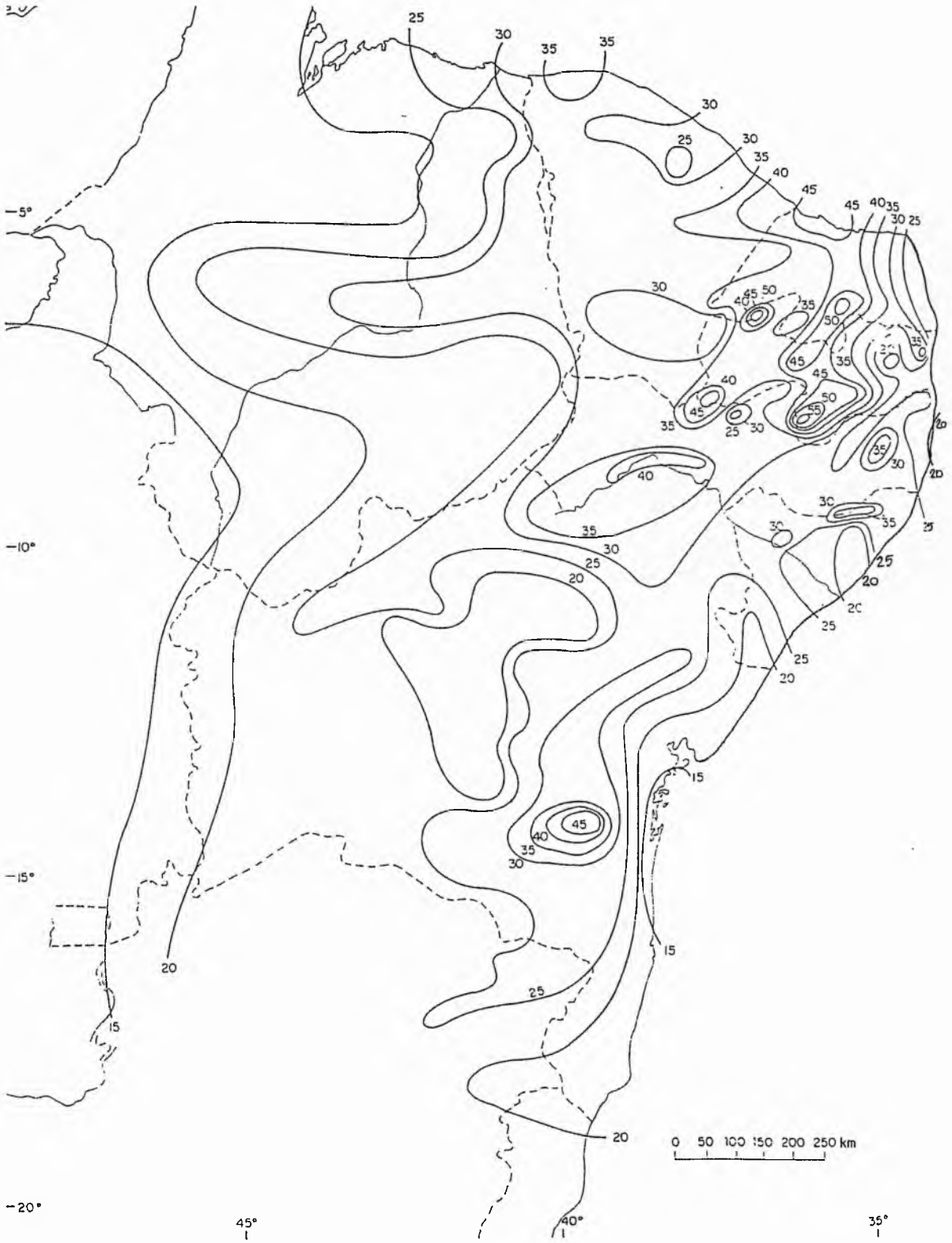

Fig. 3.5: Percentage of average yearly rainfall deviation in NE Brazil. Modified from Nimer, 1972.

TABLE 3.1: **Rainfall data for Sobral, Ceará (Brazil), during the period 1934-1952. Modified from Guerra, 1955.**

YEAR	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1934	71.7	258.8	325.8	284.3	120.7	75.5	0.1	-	4.0	-	10.4	51.6	1202.9
1935	37.1	266.8	204.9	313.3	143.1	84.9	3.6	-	-	-	-	1.7	1105.4
1936	20.4	97.4	67.6	66.1	92.6	22.5	-	-	-	0.1	-	-	366.7
1937	43.1	119.4	165.2	180.5	117.9	70.4	45.7	-	14.8	8.2	-	-	765.2
1938	30.1	65.4	416.8	237.0	104.3	2.5	5.5	-	-	1.0	1.0	-	863.6
1939	12.0	356.0	205.3	131.2	83.6	50.7	6.6	-	-	27.5	7.5	-	880.4
1940	94.0	93.1	286.4	353.3	99.6	66.6	7.4	-	-	7.5	2.0	17.3	1027.2
1941	-	84.9	241.6	165.8	63.8	9.2	21.2	-	-	-	-	-	586.5
1942	12.8	172.7	175.4	74.0	11.5	-	-	-	-	-	-	40.5	486.9
1943	42.9	16.6	288.3	140.1	59.4	16.8	2.4	-	13.5	-	-	56.7	636.7
1944	38.9	7.3	229.2	249.5	192.3	-	-	-	-	-	-	42.7	759.9
1945	120.6	451.1	329.1	243.1	138.8	40.0	18.6	-	-	-	-	6.3	1348.2
1946	98.2	192.2	270.6	198.1	15.8	39.1	-	-	-	-	4.0	23.5	841.5
1947	22.1	159.1	273.9	227.5	95.4	4.5	-	-	-	-	21.5	70.2	874.2
1948	52.7	89.0	147.7	152.4	61.4	15.6	9.7	-	-	-	-	-	528.5
1949	?	?	?	174.1	135.2	17.0	-	?	?	?	?	?	?
1950	88.5	78.8	282.4	278.0	176.0	2.3	10.5	-	-	-	-	-	916.5
1951	30.9	5.5	10.4	132.0	24.9	27.3	-	-	-	-	-	132.0	363.0
1952	12.9	81.7	244.6	179.3	157.6	19.5	-	-	-	-	-	11.2	706.8

Fig. 3.6: Annual absolute minima of temperature in NE Brazil. Modified from Nimer, 1972.

Fig. 3.7: Annual absolute maxima of temperature in NE Brazil. Modified from Nimer, 1972.

for salt leaching. According to Tricart (1972, p. 33) "here is a sure criterion to delimit the humid tropics from the semiarid zone. In the caatinga regions of Brazil [...] films of salt accumulate between the crystalline hills, indicating an insufficiency of salt leaching. Kaolinite cannot form in such circumstances." Thus the predominant clay to be found is montmorillonite, responsible for a particular kind of soils, Grumosols or Vertisols, which are very common in the interfluvial platforms across the Caatingas pediplane. Indeed, Vertisols have been regarded as the climatogenic soils of this area (Ab' Sáber, 1974 & 1977a).

Perhaps the commonest soil class are the Non-Calcic Browns (Beek & Bramao, 1968; Bautista, 1986), frequently ranging from Vertic with intermediate features to Vertisol (Figueiredo Gomes, 1981), with a textural B horizon and characteristic stones and boulders in surface. Given the nature of the region, Entisols and particularly Lithosols are very abundant, derived by weathering of parent rocks. Extensive rock outcroppings are regionally called 'lajedos', which act ecologically as desertic environments and where only succulent plants are to be found (generally *Pilosocereus gounellei* and *Encholirium* spp.). Pediments covered by a more or less continuous layer of stones (Desertic Pavements) are also frequent. Incipient soils can be found under the stone layer of some Lithosols, and pockets with thin Vertisols or moderately deep alkaline soils are frequent (Ab' Sáber, 1974) in the intermingling of soils resulting from the different erosive phases (Beek & Bramao, 1968). Some Solonetz with high concentration of clay and sodium in the B horizon occur in localized areas of Ceará and Bahia (Ab' Sáber, 1974), and in Rio Grande do Norte in more extended areas on the Mossoró river valley (Figueiredo, 1987). Also very restricted areas locally called 'salgados' (brackish) can occur, where intermittent rivers fail to reach a major river. However, it should be emphasized that it is only the exorheic character of the Caatingas drainage that prevents halomorphic soils from being a much more prominent feature of the region (Ab' Sáber, 1974 & 1977a). Also noteworthy are the presence of rather isolated areas with red soils (Dark Red Latosols, in Bautista, 1986) with a prismatic B horizon, which are mainly located in the highest areas of the intertablelands depressions (Ab' Sáber, 1974) and which represent the remnants of what has been called the 'sertão old surface' which has escaped complete pediplanation. Such red soils, also reported by Tricart

(1961), are apparently true palaeoferralitic soils, and are found in western Pernambuco, Alagoas, and Rio Grande do Norte, where they are covered by dense arboreal caatinga. The existence of these soils within a semiarid region is regarded as evidence for more humid climates in the Upper Pleistocene than those of the present-day, and they could have supported dry or even wet tropical forests (Ab' Sáber, 1974). Other important classes of soils reported from the Caatingas are the poorly studied calcimorfic soils in Ceará, Bahia and particularly Rio Grande do Norte (Andrade-Lima, 1964c; Ab' Sáber, 1974), alluvial and some hydromorphic soils related to watercourses (Ab' Sáber, 1974; Figueiredo Gomes, 1981; Figueiredo, 1983), and the deep sedimentary sandy soils usually known as Areias Quartzosas in Brazil (Quarztpsamments, 7th Appr.) which occur in the Cipó series in Pernambuco and Raso da Catarina, Bahia (Andrade-Lima, 1981).

3.4- Vegetation of the Caatingas[1]:

The Caatingas can be characterized as woodlands, both forests and scrublands, comprising mainly low, deciduous trees and shrubs, many of which present spines or thorns, microphylly and some xerophytic features. Cactaceae and Bromeliaceae are abundant whilst lianas are very scarce, and a few evergreen species (*Ziziphus joazeiro* , *Capparis yco*, *Copernicia cerifera* , *Maytenus rigida* , *Licania rigida*) also occur. The herbaceous layer is ephemeral and dominated by therophytes of the families Malvaceae, Portulacaceae and Graminae. Although succulency is found mainly in Cactaceae and Bromeliaceae, water storage organs are typical in some other cases (i.e. *Spondias tuberosa* , *Cavanillesia arborea* , *Ceiba glaziovii* , *Jacaratia* sp., *Manihot* spp., *Luetzelburgia auriculata*).

Two terms closely linked with Caatingas and their phytogeographical concept are 'agreste' and 'sertão', and a brief discussion of these is necessary to clarify the subsequent analysis. Agreste is the name applied to a narrow strip of vegetation extending between the Serra do Mar ranges in the east, where rain forests thrive, and the drier hinterlands to the west. It has an elongated shape with a general north-south direction, and it can be found from Rio Grande do Norte to central Bahia, where it is replaced in this transitional position by

[1] A more detailed analysis of caatinga floristic elements is given in Sect. 4.2.

the so-called 'mata de cipó'. The agreste enjoys a better rainfall regime (up to 1000 mm/year), and it is less subject to catastrophic droughts, since it benefits from the residual humidity of the SE winds. Its vegetation shares most of its features and species with the vast semiarid expansions to the west: deciduousness, thorny plants, abundant cacti and bromeliads on stony ground, generalized microphylly, and the more characteristic woody and succulent species in the agreste all occur in the rest of the Caatingas, such as *Schinopsis brasiliensis* , *Pilosocereus gounellei* , *Aspidosperma pyrifolium* , *Cereus jamacaru* , *Caesalpinia pyramidalis* , *Tabebuia impetiginosa* , *T. caraiba* , *Commiphora leptophloeos* , *Cnidoscolus phyllacanthus* , *Mimosa* spp. (Andrade-Lima, 1954, 1960, 1970, 1973). Thus, as Andrade-Lima demonstrated, the agreste should be regarded as part of the Caatingas, as a hipoxerophilous variant of the communities to be found to the west.[2]

The term 'sertão' is very much widely used in Brazil, from São Paulo state to the Northeast with the rather vague meaning of uncultivated place or zone, short of resources, removed from major populations and civilization (Egler, 1951). The English words such as hinterland, backlands or bush are used in a similar way. More debatable is the connotation of the word sertão in NE Brazil. Luetzelburg (1922-23) claimed that the driest and resourceless parts of the Caatingas were called sertão, while the rest was considered caatinga proper, particularly the areas where *Cereus jamacaru* , a cactus used as fodder, could be found. Egler (1951) was opposed to the use of the term sertão because of its vagueness, and proposed to separate agreste from caatinga proper, but as noted above this division has been shown to be inadequate. However, Vasconcelos (1941) and Andrade-Lima (1954, 1960, 1970) considered that the Caatingas should be simply divided into agreste and sertão , that is the transitional eastern sector on one side and the dry hinterlands on the other. This criterion is followed by the present author.

In SE Piauí there is a complex ecotone where the Caatingas meet Cerrados vegetation and varying communities can occur. There exist several degrees of transition between these major formations, i.e.

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[2] The name 'agreste' has also been applied to the very different cerrado vegetation on top of the Chapada do Araripe, Ceará.

(a) semideciduous cerrado, with some few caatinga elements, (b) the 'carrasco' or 'catanduva', with about equal proportion of cerrado and caatinga elements but also with some exclusive elements, and (c) typical caatinga with sparse cerrado elements (Eiten, 1972; Andrade-Lima, 1978). It is notable, however, that in this area the cerrado vegetation is largely confined to sedimentary sectors with sandy soils, while the Caatingas tend to appear in sectors affected by diabasic rock outcroppings with much more fertile soils (Andrade-Lima, 1978; Emperaire, 1983), even though the rainfall regime is the same at *ca* . 1000 mm/year.

There have been several attempts to classify the vegetation of the world according to its physiognomy (Schimper, 1903; Drude, 1913; Trochain, 1957; Ellenberg & Mueller-Dombois, 1967). A number of authors have also devised hierarchical physiognomic classifications of vegetation at a continental (Beard, 1944 & 1955; Smith & Johnston, 1945; Eiten, 1974) or Brazilian level (Castellanos, 1960; Rizzini, 1963; Veloso & Góes Filho, 1982; Eiten, 1983). No attempt is made here to analyse these systems, since the emphasis of this study is on the floristic links of the Caatingas, but probably Eiten (1974 & 1983) provides the most detailed and useful survey of the different structural types of the Caatingas vegetation. At the other extreme, it is very difficult to accept the use of the word steppe ('estepe') to denominate this formation as employed by Radambrasil (Veloso & Góes Filho, 1982), taken on board from the Yangambi Agreement (Trochain, 1957). The Russian and Siberian steppes are grasslands, sometimes with scattered low shrubs, which undergo a severe winter with frozen soil, and its use for the Caatingas has already been challenged by Kuhlmann (1974). Once again, however, this is a purely geographic term and its use for vegetation physiognomy has been rejected (Tanfiljew, 1905; Cain & Castro, 1959, p. 48).

The physiognomy of the Caatingas vegetation is very variable, depending on the rainfall regime and soil type, ranging from a tall, dry forest up to 15-20 m high, e.g. the 'arboreal caatinga' (the true caatinga of the Tupí indians, according to Andrade-Lima) found scattered from Bahia (Andrade-Lima, 1975) and Minas Gerais (Magalhães, 1961) to Rio Grande do Norte (Andrade-Lima, 1964c) on somewhat better soils and in more humid localities, to rock outcroppings with scattered and sparse low shrubs, cacti and bromeliads in crevices. Intermediate

physiognomic forms are numerous but they can be reduced to a few generalized types, such as 'open arboreal caatinga with an open shrub layer', 'shrubby-arboreal caatinga with a closed shrub layer', 'closed thorn scrub with scattered overtopping low trees' – which is perhaps the most common kind of present-day caatinga community (Eiten, 1974 & 1983), 'closed thorn scrub', 'open shrubby caatinga' (common in areas with extended shallow soils), 'scrub savanna with shortgrass layer' ('seridó'; Andrade-Lima, 1966a; Eiten, 1983), and '*Copernicia* palm groves' along intermittent rivers mainly in NW Caatingas province.

Another group of authors have tried to analyse and identify the different units of vegetation in the Caatingas, following floristic-physiognomic criteria but with most of the weight on the floristic composition of the communities. A landmark effort in this sense was that by Luetzelburg (1922-23) in his 'Estudo Botânico do Nordeste', a work based on the author's extensive travels throughout the Caatingas over a 10 year period. His classification, although interspersed with taxonomical and conceptual mistakes (Andrade-Lima, 1954), can still be seen as the framework for the overview by Andrade-Lima (1981). Luetzelburg divided the Caatingas roughly into two classes: 1) shrubby or scrub caatinga ('caatinga arbustiva'), and 2) arboreal caatinga or caatinga forest ('caatinga arbórea'), which he then subdivided in several groups:

Class 1: Scrub Caatinga

1.1- *Euphorbia - Croton - Caesalpinia* caatinga
1.2- *Mimosa - Caesalpinia* caatinga
1.3- *Spondias - Caesalpinia - Cnidoscolus* caatinga
1.4- *Cereus - Mimosa - Spondias - Bromelia* caatinga
1.5- *Combretum - Aspidosperma - Caesalpinia* caatinga
1.6- *Jatropha - Cnidoscolus - Mimosa* caatinga
1.7- *Chorisia - Mimosa - Manihot* caatinga
1.8- Caatinga-carrascal or 'caatinga suja' [literally: dirty caatinga]
1.9- Caatinga serrana (mountain caatinga)

Class 2: Arboreal Caatinga

2.1- *Aspidosperma - Schinopsis* (sub *Melanoxylon*) - *Piptadenia* caatinga

2.2- *Chorisia - Piptadenia - Spondias* caatinga

2.3- *Cocos coronata - Copernicia cerifera - Cocos comosa* (sub *Mimosa*) caatinga

Some of these units have been recognized or slightly modified by Andrade-Lima (1981), such as groups 1.3 or 2.1 and 2.2 . In group 2.1 *Melanoxylon* is in fact *Schinopsis* , one of the common mistakes in this work, while *Mimosa* in group 2.3 must be a compilation error for *Cocos (=Syagrus) comosa* , the catolé palm, which occasionally occurs in Caatingas (Glassman, 1987). Group 1.8 is clearly what is known as 'carrasco' or 'catanduva' (Andrade-Lima, 1978; Emperaire, 1983; Oliveira et al., 1988), a transitional type of vegetation with the Cerrados in SE Piauí which, whilst it includes species of caatinga, is floristically, physiognomically and phenologically (semideciduous) closer to cerrado vegetation, and it is not accepted here as part of the Caatingas. The term 'suja' alludes to the fact that these communities have mixed elements of the Cerrados formation. Group 1.9 refers to low or dwarfed scrubby vegetation on inselbergs and dry sierras, mainly on rock outcroppings, but not to arboreal caatinga which can occur on less dry slopes nor to the wet 'brejos' which occur in the east of the Caatingas and are floristically excluded from the province. Hueck (1972) criticised Luetzelburg's classification, and presented it in his own work "only for historical reasons", but in fact his strictures are rather insubstantial, and he simply succeeded in having Luetzelburg's mistakes perpetuated and compounded, including the most obvious errors such as the misidentification of *Schinopsis* for *Melanoxylon* .

Rizzini (1963), in his floristic-phytosociological study of Brazilian vegetation, concluded that the Caatingas should be treated as a subprovince of what he called the 'Atlantic Province', on account of what he regarded as the very close floristics links between the Caatingas and the coastal forests. Thus, Rizzini's 'Northeastern Subprovince' includes:

1- Agreste sector: deciduous xerophilous forests;

2- Sertão sector: thorny and succulent scrub, which also involves three internal districts, 2.1: *Copernicia cerifera* palm consociations; 2.2: higromontane rain forests ('brejos'); 2.3: xeromontane savannas and woodlands on sedimentary surfaces ('agreste' of Araripe);

3- Seridó sector: semiarid scattered scrub and succulent scrub;

4- Fernando de Noronha Island: agreste type of woody vegetation, with a six months long dry season.

Rizzini (1963) grouped together disparate kinds of vegetation which have little in common with the Caatingas as accepted by most authors, either floristically or physiognomically, such as the cerrado vegetation of the Chapada do Araripe and coastal taboleiros, and the rain- and cloudforests of the 'brejos'.

Veloso (1964) also presented a vegetation map of the Northeast, but he divided the region into subregions (which he called physiognomical areas) based on geographical criteria. The result is inadequate for the phytogeographical synthesis which was intended since, although most of the Caatingas are grouped together, several facies are separated into different so-called 'subregions', e.g. the agreste is fragmented and sometimes confused with cerrado vegetation but never associated to the Caatingas. For the bulk of the Caatingas, denominated Semiarid Vegetation of Eastern Northeast, from which Veloso correctly detached the Serra do Araripe cerrado, the vegetation of the pediplains was classified as follows:

a- 'caatinga formation'[3]: predominantly deciduous thorny vegetation. This was further subdivided into three subclasses based on their physiographic position on the terrain (instead of their floristics): (a.1) sandy tablelands caatinga, with dense shrubby vegetation interspersed with trees; (a.2) caatinga of the depressions, shrubby with occasional trees; (a.3) caatinga on inselbergs and arid depressions, with vegetation in scattered clumps and spiny succulents.

b- 'forest formation': deciduous, thorny, arboreal vegetation interspersed with evergreen trees. This evidently refers to arboreal caatinga, as described by Andrade-Lima (1981), but the presence of evergreen trees cannot possibly be used to characterize it since they occur throughout the Caatingas (e.g. *Ziziphus joazeiro*).

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[3] Veloso (1964) misused the term "formation", which is a physiognomic vegetation unit with similar structure and a characteristic essential habitat, and it is independent of the flora (Beard, 1944, 1955). A "caatinga formation" would be possible only if it had a physiognomy exclusive to it, which is certainly not the case. The Caatingas can easily fit into Beard's (op.cit.) "thorn woodland", and so does the Chaco. At the other extreme, "forest formation" is too ambiguous.

TABLE 3.2: **Main units of vegetation and community types of the Caatingas (modified from Andrade-Lima, 1981)**

UNIT		VEGETATION TYPE	PHYSIOGNOMY & LOCATION	SUBSTRATUM
I	1	*Tabebuia-Anadenanthera-Astronium-Cavanillesia-Schinopsis*	Tall caatinga forest; N Minas Gerais & S central Bahia	limestone Bambuí or Pre-Cambrian crystalline rocks
II	2	*Astronium-Schinopsis-Caesalpinia*	Median caatinga forest; most of the centre of the province	mainly Pre-Cambrian crystalline rocks
II	3	*Caesalpinia-Spondias-Commiphora-Aspidosperma*	Median caatinga forest; drier area than preceding	mainly Pre-Cambrian crystalline rocks
II	4	*Mimosa-Syagrus-Spondias-Cereus*	Low caatinga forest; N central Bahia	mainly P.Cambrian crystalline rocks
III	5	*Pilosocereus-Poeppigia-Dalbergia-Piptadenia*	Low caatinga forest; sandy soils from the Cipó series	Cipó series sandstone rocks
II	6	*Cnidoscolus-Commiphora-Caesalpinia*	Open arboreal caatinga;SW Ceará and medium dry areas with loose, acid soils	mainly P.Cambrian crystalline rocks
IV	7	*Caesalpinia-Aspidosperma-Jatropha*	Shrubby caatinga; drier areas in the São Francisco valley	mainly P.Cambrian crystalline rocks
IV	8	*Caesalpinia-Aspidosperma*	Open shrubby caatinga; Cariris Velhos, Paraíba	mainly P.Cambrian crystalline rocks
IV	9	*Mimosa-Caesalpinia-Aristida*	Open shrubby caatinga (seridó); Rio Grande do Norte & Paraíba	mainly P.Cambrian crystalline rocks
IV	10	*Aspidosperma-Pilosocereus*	Open shrubby caatinga; Cabaceiras, Paraíba	mainly P.Cambrian crystalline rocks
V	11	*Calliandra-Pilosocereus*	Open shrubby caatinga; small, restricted scattered areas with gravelly soils	mainly P.Cambrian metamorphic rocks
VI	12	*Copernicia-Geoffroea-Licania*	Fringe caatinga forest; river valleys of Ceará, Piauí & Rio Grande do Norte	mainly alluvial soils
II	13	*Auxemma-Mimosa-Luetzelburgia-Thiloa*	Median caatinga forest; W Rio Grande do Norte & central Ceará	mainly P.Cambrian crystalline rocks

Schnell (1966) also proposed a simplified classification of the Caatingas, with (1) dense dry forests with some swollen-trunk tree species, (2) dense scrub with large Cactaceae, (3) open scrub with a 'steppic' character, and (4) diffuse caatinga with spaced bushes in the driest areas. Hayashi & Numata (1976) attempted to classify the Caatingas on the basis of life forms, but this study was too reduced in geographical scope to be of value.

The most coherent and comprehensive work on this vegetation is that by Andrade-Lima (1981). This overview, which treats the Caatingas as a Dominium (a chorionomic unit equivalent to the more widely used Province unit, Takhtajan, 1986), builds on Luetzelburg's substantial pioneer reports, but is also the result of Andrade-Lima's numerous previous studies which dealt with particular areas of the Caatingas as a whole, and especially with the vegetation of the state of Pernambuco (Andrade-Lima, 1953, 1954, 1960, 1961, 1964b, 1964c, 1966a, 1966c, 1967b, 1970, 1971, 1973, 1975, 1977, & 1978). Essentially, Andrade-Lima's concept of the Caatingas, which was basically a floristic conception of the province without losing contact with the physiognomy and ecology of the vegetation, is the one followed here.

Table 3.2, modified from Andrade-Lima (1981), shows in a condensed manner the main units of vegetation and community types for the Caatingas, which includes a new vegetation type proposed here. A brief discussion on the units follows:

UNIT I: Veg. Type 1, Tall Caatinga Forest. It is entirely agreed that this is a member of the province; although the physiognomy of this community is very distinct to that of other vegetation types within the Caatingas, the clear-cut leafless period and above all the floristic composition firmly link this forest-type to the province. Genera and species dominant here are common throughout the Caatingas, and sometimes they will appear only in caatinga areas (e.g. *Commiphora leptophloeos*). Certainly some alien mesophytic species are also to be found in this type of forest, but they are always only minor members of the community. See also Magalhães (1961), Andrade-Lima (1971, 1975, 1977), Magalhães & Ferreira (1976, *apud* Andrade-Lima, 1981), Ratter et al. (1978). In

Ceará a kind of mid-slope Mata Seca (dry forest) or mesophilous forest has been described by Figueiredo (1984) which lack the swollen-trunk Bombacaceae but in all other respects seems to be arboreal caatinga with some mesophilous elements. Out of 16 species mentioned by this author, 10 are members of caatinga forests and an eleventh is very occasionally found (*Syagrus comosa*). In E and SE Bahia the 'mata de cipó' (lianas forest) seems to comprise a wide transition between the coastal rainforests and the inner Caatingas, and consists of different types of dry deciduous forests and subhumid semideciduous forests. At least some facies of them contain typical species of caatinga (Andrade-Lima, 1971). There is very little knowledge about this formation, a fact also remarked by Bégué (1967 & 1968), but some short but accurate descriptions (Andrade-Lima, 1966a, 1971; see also Noblick, *in litt..*, in Plowman, 1987) allow for the inclusion of at least some of the dry forests as arboreal caatinga.

UNIT II: Veg. Types 2, 3, 4 & 6 (for veg. type 13, see below), typical Median Caatinga Forest, with variable density in the tree layer, 7-15 m tall. Very widespread and common unit of vegetation throughout NE Brazil, probably with a multitude of facies of which Andrade-Lima commented on four. Several of the dominant species in Unit I also appear as scattered elements in these kind of communities, such as *Anadenanthera colubrina* var. *cebil* , *Commiphora leptophloeos* , *Astronium urundeuva* , *Schinopsis brasiliensis* , and *Amburana cearensis* . Most of Andrade-Lima's papers carry at least one description of this vegetation type; also in Figueiredo Gomes (1981), Figueiredo (1983 & 1987), Figueiredo & Fernandes (1985), Carvalho (1986).

UNIT III: Veg. Type 5, Low Caatinga Forest. A very distinct unit, described in somewhat more detail in Egler (1951) and Andrade-Lima (1960, 1970). Very restricted in area to the sandy soils in south-central Pernambuco (Moxotó tableland) and northern Bahia (Raso da Catarina), and characterized by the species *Pilosocereus piahuiensis* , *Poeppigia procera* , *Dalbergia cearensis* , *Pilosocereus tuberculatus* . The palm *Syagrus coronata* ('ouricouri') can also occur here in fairly big populations, but

although Egler and Andrade-Lima (*op . cit* .) mentioned the species previously, the latter author failed to include it in his overview (Andrade-Lima,1981).

UNIT IV: Veg. Types 7, 8, 9 & 10, Dense or Open Shrubby Caatinga. This is the most widespread vegetation type nowadays, and it is still a contentious matter as to what extent it is entirely natural or man-induced. Although the influence of man in the area has been marked, to consider this unit as a completely secondary vegetation would seem to grossly underestimate the homeostatic ability of these ecosystems. On the contrary, Carvalho (1986) for instance found stability as the main feature of the Caatingas of western Pernambuco for the period 1955-1983, together with a moderate expansion of agriculture, despite the probably heavy human pressure in the intervening years. Furthermore, it is a striking coincidence that this Unit IV corresponds geographically to the driest areas within the province, such as the São Francisco valley (type nº 7), the 'seridó' (type nº 9), or the vegetation of the Cariris Velhos, Paraíba (types nº 8 & 10, in the Borborema Plateau), with the lowest rainfall record of the Caatingas (Cabaceiras: 252.4 mm/year; Figueiredo Gomes, 1981). Moreover, there is a direct correlation between rainfall, soil depth, and soil permeability to height and density of the community (Sampaio et al., 1981), which would allow one to predict the vegetation type to be found in one area. This unit consists typically of scattered trees of species such as *Amburana cearensis*, *Spondias tuberosa* , *Aspidosperma pyrifolium* , in a shrubby matrix of *Caesalpinia* spp., *Mimosa* spp., *Jatropha* spp., and *Acacia* spp.. More information on this unit is available in Vasconcelos (1941), Egler (1951), most of Andrade-Lima's papers, Anon. (1980), Figueiredo Gomes (1981), Figueiredo (1987).

UNIT V: Veg. Type 11, Low Open Shrubby Caatinga. Very restricted in surface and area, on shallow sandy or gravelly soil under a long dry period (8-9 months). Dominated by *Pilosocereus gounellei* , *Calliandra depauperata* and *Melocactus bahiensis* , the unusual small height of this community (0.70-1 m) seems to be caused by grazing (Andrade-Lima, 1981). Only reported in the literature by

Andrade-Lima (*op . cit* .), its status is doubtful to the present author who visited one small stand of this community in Ceará. It seems very probable it is simply the result of heavy overgrazing and therefore of indirect anthropic influence, but further research is necessary.

UNIT VI: Veg. Type 12, fringe forest along watercourses mainly in Piauí, Ceará and Rio Grande do Norte. Physiognomy dominated by the palm *Copernicia cerifera* ('carnaúba'), accompanied by *Licania rigida* , *Geoffroea striata* , *Sideroxylon obtusifolium* , *Erythrina velutina* , *Ziziphus joazeiro* , *Capparis yco* . The dominant palm-tree species, the Chrysobalanaceous tree *Licania rigida* and perhaps *Capparis yco* are not only endemic to the Caatingas but also to this limited environment , where there is relatively constant supply of water from the water-table during droughts, and it is flooded in the rainy season. The very slow dessication of heavy alluvial soils causes salinization, a rather rare phenomenon in the Caatingas. Descriptions of this vegetation type can be found in Andrade-Lima (1954, 1964c, 1978), Emperaire (1983), Figueiredo (1987).

UNIT II: Veg. Type 13, Median Caatinga Forest. This comprises a new addition to Andrade-Lima's classification which is proposed here. The existence of such a unit was indicated by Andrade-Lima (1981) who commented: "In the states of Rio Grande do Norte and Ceará, this unit {II} presents a facies (which may be an independent unit of its own to be recognized after further studies) in which *Auxemma oncocalyx* is one of the dominant species". During field work in Ceará the present author had the opportunity to visit several stands of this community, and can confirm that it should constitute a separate entity since it shows a distinct subset of species which are largely restricted to this vegetation type: *Auxemma oncocalyx* , *Mimosa caesalpiniifolia* ('sabiá'), and in piedmont areas *Luetzelburgia auriculata* ('pau mocó') (Lima, 1982), and, less consistently, *Thiloa glaucocarpa* . The community is sometimes dominated by other widespread species such as *Astronium urundeuva* , *Anadenanthera colubrina* var. *cebil* ,

Aspidosperma pyrifolium , *Caesalpinia pyramidalis,* which share the canopy with *Auxemma oncocalyx* .

Plate 3.1: The caatinga vegetation at Parnamirim, Pernambuco, Brazil. Top: 'angico' and 'jamacaru' predominate in open shrubland. Center: shrubby caatinga with sparse *Commiphora leptophloeos*. Bottom: the 'umbú', *Spondias tuberosa*.

4. WOODY AND SUCCULENT SPECIES FLORISTIC LISTS

To evaluate the floristic links between the Chaco and the Caatingas vis-à-vis the rest of seasonal forests and woodlands of South America basic floristic lists of both provinces were needed. These have been built up based on the following sources:

a- Exsiccata obtained on loan from diverse Herbaria (G, GH, A, E), plus visits to K, BM, E, UB, UEC, IPA, EAC and UNR.

b- Exhaustive checks on taxonomic literature and verification of identity of those species cited in floristic lists and phytogeographical accounts.

c- Field experience of the present author.

In general all species cited in the following tables have been reported in at least two reliable floristic studies or phytogeographical accounts, whereas the sole mention of a taxon in monographic treatments is taken as enough evidence of its occurrence in the area under study.

4.1- Woody and succulent species of the Chaco *s.s.* :

In the floristic list of Chaco *s.s.* woody and succulent species, those indicated with an asterisk (*) correspond to taxa known to occur only in the Sierra Chaco within the scope of the Chaco as here understood (see Ch.2). The taxa indicated with a capital m letter (M) are regarded as Monte intruders into the Chaco, in no way typical chaquenian species. In the 'Main Synonym' column the names between brackets ([...]) are common identification mistakes or binomials wrongly applied to the entities shown in the 'Species Name' column, not to be treated as taxonomic synonyms. In the 'References' column, h.s. stands for 'herbarium specimens' in those cases in which exsiccata have been taken by the present author as evidence of the alleged presence of the species in the area.

Fly Nº	Gen Nº	Sp Nº	SPECIES NAME	MAIN SYNONYM	VERNACULAR NAME	REFERENCES
1			ACHATOCARPACEAE			
	1	1	*Achatocarpus praecox* Gris.	*A. nigricans* Triana	palo de tinta, palo mataco, ruma caspi, tala negro	378, 315, 9, 135, 281, 67
2			ANACARDIACEAE			
*	2	2	*Lithraea ternifolia* (Gillies)Barkley	*L. gilliesii* Gris.	molle blanco, molle de beber, chichita, etc.	378, 47, 136, 281
	3	3	*Schinopsis balansae* Engler	*Quebrachia morongii* Britton	quebracho colorado chaqueño, q. c. correntino, q. chaq., urunday	378, 304, 97, 67
		4	*Schinopsis cornuta* Loes.		soto negro	304

*		5	*Schinopsis haenkeana* Engler	*S. marginata* Engler; *S. lorentzii* **var.** *marginata* (Eng.)Cabr.	horco quebracho, q. colorado del cerro, q. serrano, q. cordobés	378,136, 304, 281
		6	*Schinopsis heterophylla* Rag.& Cast.		quebracho colorado mestizo	378, 323
		7	*Schinopsis quebracho-colorado* (Schlecht.) Barkley & Meyer	*S. lorentzii* (Gris.) Engler	quebracho, q.macho, q.coronillo, q.colorado, q.col.santiagueño	378,109,315, 413, 304,97, 281, 67
	4	8	*Schinus bumelioides* I.M.Johnston	*S. myrtifolius* Cabr.	molle, m.blanco, m.colorado, m. negro, m.chico, moradillo	45, 315, 281
		9	*Schinus fasciculatus* (Gris.)Johnst.	*S. polygamus* f. *fasciculatus* Cabrera	molle, m.blanco, m.colorado, m. santiagueño,trementina, etc.	378, 45, 7, 281, 67
			var. *arenicola* (Haum.) Barkley	*S. p.* f. *arenicola* Cabr.	molle, m.blanco, m.de incienso	45, 315
*		10	*Schinus molle* L. **var.** *areira* (L.)DC.	*S. areira* L.	aguaribay, molle	378, 45, 97
		11	*Schinus piliferus* I.M.Johnston		molle, m.blanco, m.criollo, etc.	45, 97
			var. *boliviensis* (Barkl.)Barkley		chirimolle, molle, m.de incienso	45, 315
*		12	*Schinus praecox* (Gris.)Speg.	*Duvaua praecox* Gris.	molle de curtir, moradillo	45, 281
3			APOCYNACEAE			
	5	13	*Aspidosperma quebracho-blanco* Schlechtendal	*A. quebrachoideum* Rojas Acosta	quebracho blanco, q.morotí, cacha-cacha, q.branco	378, 315, 136, 97, 281,286
		14	*Aspidosperma triternatum* Rojas Acosta	*A. chakensis* Speg., *A. horko-kebracho* Speg.	quebracho negro, q.blanco chico, q.blanco lagunero	378, 315, 136,286
	6	15	*Vallesia glabra* (Cav.)Link.	*Rawolfia glabra* Cav.	ancoche, engorde, teta de gata	315,136,97,281
4			ARECACEAE			

	7	16	*Copernicia alba* Morong	*C. australis* Becc.	carandá, caranday, c.-hú (palma negra), c.-morotí (p.blanca), c.-puitá (p.colorada)	378,93,109,315, 379,9
	8	17	*Trithrinax biflabellata* Barb. Rodr.		carandillo, palma	134,97,354,67
		18	*Trithrinax campestris* (Burm.) Drude & Gris.		palma, palmera, carandilla, caranday	136,97,354,281
5			ASCLEPIADACEAE			
	9	19	*Marsdenia castillonii* Lillo ex Meyer		mandioca, yuca, batata d. monte	38
6			ASTERACEAE			
*	10	20	*Baccharis articulata* (Lam.)Pearson		carqueja, carquejilla	281, 91
*		21	*Baccharis flabellata* Hook. & Arn.			413, 281, 91
*		22	*Baccharis myrtilloides* Grisebach			281, 91
		23	*Baccharis notosergila* Grisebach		carqueja	413, 7, 97
		24	*Baccharis salicifolia* (R.& P.)Pers.		suncho, chilca, chilca blanca	93,315,413,97
	11	25	*Cyclolepis genistoides* Gill. ex Don		palo azul, matorro	315,379,9,281
*	12	26	*Eupatorium buniifolium* Hook. & Arn.		romerito	97,281,91
*		27	*Eupatorium viscidum* Hook. & Arn.			134,413,281
*	13	28	*Flourensia campestris* Gris.		chilca	134,413,281
*		29	*Flourensia oolepis* Baker		chilca	281
*	14	30	*Heterothalamus alienus* OK.		romerillo	413,379,97,281
	15	31	*Hyalis lancifolia* Baker			97
*	16	32	*Ophryosporus axilliflorus* Hieron.			97

*	17	33	*Proustia ilicifolia* Hook. & Arn.	*P. pungens* Poepp.	altepe, huañil, sacha rosa, rosa del monte, chilca de Castillo	134, 281
	18	34	*Tessaria absinthioides* (H.& A.)Cabr.		chilca, suncho, s. negro	93, 413, 9
		35	*Tessaria dodoneaefolia* (H.& A.)Cabr.		chilca negra, suncho negro	378,93,315,379, 314,9
		36	*Tessaria integrifolia* Ruiz & Pavón		palo bobo, aliso	93,9,97
7			BERBERIDACEAE			
*	19	37	*Berberis hieronymi* Schn.			340, 281, 91
		38	*Berberis ruscifolia* Lam.		quebrachillo/a, sacha uva, uvilla, palo azul, talilla	340, h.s.
8			BIGNONIACEAE			
	20	39	*Dolichandra cynanchoides* Cham.	*Macfadyena cynancho ides* (Cham.) Morong	sacha-huasca, teyú-igsipó, malagraik-laachí	416, 164,413,281
	21	40	*Mansoa truncata* Sprague	*Petastoma truncatum* (Sprague)Hassler		416, 134,164
	22	41	*Pithecoctenium cynanchoides* DC.	*P. clematideum* (Gris.)Gris.	chacha, trompetilla de Venus, peine de mono, caí-quiguá, etc.	416,134, 164,413, 281,67
	23	42	*Tabebuia nodosa* (Grisebach)Grisebach	*Tecoma nodosa* Gris.; *Bignonia morongii* Brt.	toratai, tororotay, palo cruz, uíñaj, Martín Gil, labón	416, 134, 378,315, 164,413, 281,67
9			BOMBACACEAE			

	24	43	*Ceiba chodatii* (Hassler) Gibbs & Semir comb. ined.	*Chorisia insignis* Kth.	palo borracho, yuchán, painero, algodonero, etc.	134,378,109,315, 9,97,67, Gibbs (pers.comm.)
10			BORAGINACEAE			
	25	44	*Cortesia cuneifolia* Cav.		campa	413,97,281,64
11			BROMELIACEAE			
	26	45	*Bromelia hieronymi* Mez		chaguar blanco, cardo vid	315,9,97,281, 159, 67
		46	*Bromelia serra* Grisebach		chaguar, cardo gancho	109,315,9,67
		47	*Bromelia urbaniana* (Mez)L.B.Smith	*Deinacanthon urbanianum* (Mez)Mez	chaguar salado, chaguarillo	109,315,9, 281
*	27	48	*Deuterocohnia longipetala* (Baker)Mez		chaguar	432, 281
	28	49	*Dyckia ferox* Mez		chaguar	432
		50	*Dyckia floribunda* Grisebach	*D. chaguar* Castell.	chaguar	9, 432, 281
		51	*Dyckia ragonesei* Castellanos		chaguar	432
		52	*Dyckia tweediei* Mez		chaguar	432
*	29	53	*Puya spathacea* (Gris.)Mez		chaguar del burro, chagual	432, 281
12			BUDDLEJACEAE			
	30	54	*Buddleja brasiliensis* Jacq. ex Spreng.		palo blanco	134,413,281
*		55	*Buddleja cordobensis* Grisebach		palo blanco	413,379,281,91
*		56	*Buddleja mendozensis* Benth.		palo blanco, salvilora	134,413,281
		57	*Buddleja stachyoides* Cham.& Schlecht.			134,413

13			CACTACEAE			
*	31	58	*Acanthocalycium violaceum* (Werd.) Backeberg			238, 281
	32	59	*Castellanosia caineana* Cárd.			159
	33	60	*Cereus æthiops* Haworth		víbora	76, 281, 67
		61	*Cereus comarapanus* Cárd.			159
		62	*Cereus validus* Haworth	*C.forbesii* Otto	ucle	76,378,93,109, 315,9,281,67,159
	34	63	*Cleistocactus baumannii* (Lem.)Lemaire	*C. flavispinus* (K.Sch.) Back.; *Cereus baumannii* Lem.	uvillinche, cola de gato	76,378,315,413, 238,281,159,240
		64	*Cleistocactus bruneispinus* Backeberg			159
		65	*Cleistocactus smaragdiflorus* (Web.)Br.& Rose	*Cereus smaragdiflorus* Weber	uvillinche, cogote de suri	76,109,315,9, 240
	35	66	*Echinopsis chacoana* Schütz			159
		67	*Echinopsis leucantha* (Gillies)Walper	*E.melanopotamica* Spg		76,93,281,157
		68	*Echinopsis minuana* Spegazzini			76,314
		69	*Echinopsis schaferi* Br. & Rose			76, 109, 314
	36	70	*Eriocereus bonplandii* (Parm.)Ricc.	*Harrisia bonplandii* (Parm.)Br. & Rose	ulúa	76,109,315,9, 159
		71	*Eriocereus guelichii* (Speg.)Berg	*Harrisia g.*(Sp.)B.& R.		76,378,97,159

		72	*Eriocereus martinii* (Lab.)Ricc.	*Harrisia martinii* (Lab.)Br.& Rose		76,378,314,97, 159
		73	*Eriocereus pomanesis* (Web.) ?	*Harrisia pomanensis* (Web.) Br.& Rose	ulúa	76,109,315,9, 281,67
		74	*Eriocereus tortuosus* (Forb.)Ricc.	*Harrisia t.*(Forb.)B.&R.		76,159
*	37	75	*Gymnocalycium capillensis* Hosseus			281
M		76	*Gymnocalycium delactii* (K.Sch.)Hoss.			281
		77	*Gymnocalycium friedrichii* (Werd.)Paz. **var.** *moserianum* Paz.			159
			var. *albiflorum* Paz.			159
		78	*Gymnocalycium megatae* Y. Ito			159
		79	*Gymnocalycium mihanovichii* (Fric & Gürke) Br. & Rose	*Echinocactus mihanovichii* Fr & Gür		76,159
*		80	*Gymnocalycium multiflorum* (Hooker) Br. & Rose	*Echinocactus multiflorus* Hooker		76, 379
		81	*Gymnocalycium pflanzii* (Vaup.)Werd.			159
		82	*Gymnocalycium ragonesei* Castellanos			93,379,281
	38	83	*Monvillea cavendishii* (Monv.)Br.& Rose	*Cereus cav.* Monv.; *M. paxtoniana* (Mon.)Bor.		76,378,109,315, 238,159
		84	*Monvillea spegazzinii* (Weber)Br.& Rose	*Cereus speg.* Weber; *C. anisitsii* K.Sch.		76,378,109,315, 159
	39	85	*Opuntia aurantiaca* Lindley			76, 159

		86	*Opuntia brunnescens* Br. & Rose			76, 159
		87	*Opuntia chakensis* Spegazzini	*O.bonaerensis* Speg.?		76,378,109,314, 97,159
		88	*Opuntia colubrina* Castellanos			109,379,314
		89	*Opuntia discolor* Br. & Rose			76,315,9
		90	*Opuntia kiskaloro* Spegazzini		quiscaloro	76,315,9,281
		91	*Opuntia pædiophila* Castellanos			413,379,281,157
		92	*Opuntia quimilo* Schumann		quimil	76,378,93,315, 9,97,281,67
		93	*Opuntia retrorsa* Spegazzini	*O. platynoda* Griffiths	tuna de las cabras	76,378,109,315, 314,159
		94	*Opuntia salagria* Castellanos			159
		95	*Opuntia salmiana* Parmentier	*O. spegazzinii* Weber; *O. albiflora* Schumann	llora tigre	76,378,109,315, 7
		96	*Opuntia sulphurea* G. Don	*O. pampeana* Speg.; *O. vulpina* Weber	tuna de perro	76,378,315,9, 238,281,157,159
	40	97	*Pereskia sacharosa* Grisebach	*P. moorei* Br.& Rose	sacha-rosa, cuguchi, guyapa	76,9,97,260
M	41	98	*Pterocarpus tuberosus* (Pfeiffer)Br.& R.	*P. kuntzei* Schum.		76,281,157
	42	99	*Quiabentia pflanzii* (Vaupel)Berger	*Q. chacoensis* Back.; *Pereskia pflanzii* Vaup	sacha-rosa, amendacaru, achuma, tunilla, iutang, nujuck	108,109,315,9, 159
	43	100	*Setiechinopsis mirabilis* (Speg.) Backg. ex de Haas	*Echinopsis mirabilis* Spegazzini		76,90,379,238, 157

	44	101	*Stetsonia coryne* (Salm-Dyck) Br.& Rose	*Cereus coryne* Salm-Dyck	cardón	76,378,93,109, 315,238,281,159
*	45	102	*Trichocereus andalgalensis* (Web.)Hos.	*Cereus andalg.* Weber		239
*M		103	*Trichocereus candicans* (Gill.)Br.& R.	*Cereus candicans* Gill.		76,239,281
		104	*Trichocereus lamprochlorus* (Lem.) Br. & Rose	*Cereus lamprochlorus* Lemaire		76,239
		105	*Trichocereus spachianus* (Lem.)Ricc.	*T.santiaguensis*(Sp.)Bk		76,239
M		106	*Trichocereus terscheckii* (Parm.)Br.&R.	*Cereus terscheckii* Pm.	cardón grande, siski?[1], cholo?[1]	76,315[1],9[1],239
*		107	*Trichocereus thelegonus* (Web.)Br.&R.	*Cereus thelegonus* Web	cola de león	76,239
14			CAPPARIDACEAE			
	46	108	*Capparis atamisquea* O. Kuntze	*Atamisquea emarginata* Miers	atamisqui/e, matagusanos, mata negra,leña hedionda	378,197,315,9, 281, 97
		109	*Capparis retusa* Grisebach var.*retusa*	*C. cynophallophora* L. **var.** *retusa* (Gris.)OK	sacha poroto, ibirá-pororó, ababán	378,197,109,315, 9, 67
			var. *velutina* Hauman			197
		110	*Capparis salicifolia* Grisebach		sacha sandía, sandía hedionda, sandía de cabra	378,197,109,315, 97,67
		111	*Capparis speciosa* Grisebach	*C. pruinosa* Griseb.	sacha limón, s. naranjo, palo / bola verde, naranjillo, payaguá naranjo, meloncillo, amarguillo	378,197,109,315, 97,67

[1] Both 315 and 9 cited in fact *T. lamprochlorus* for E Salta (Argentina) and as an arboreal cactus, under the vernacular names "siski" or "cholo", but this species is not arboreal nor it is known to occur in that area (see Kiesling, 1978). Probably they must have referred to the candelabra-like*T. terscheckii* (Parm.) Br. & Rose.

		112	*Capparis tweediana* Eichler		sacha membrillo, mboy-curé-caá yerba de la comadreja, cayampa, meloncillo, sacha coca	378,197,109,315, 97,67
15			CARICACEAE			
	47	113	*Jacaratia corumbensis* Kuntze	*J. hassleriana* Chod.	yacón, Akol-yacón, cipoy	104,308,379,43
16			CELASTRACEAE			
	48	114	*Maytenus spinosa* (Gris.)Lour.&O'Don.	*Moya spinosa* Gris.	abreboca, sacha mistol, molle negra, piquillín negro, p. de loro	378,315,413,97, 281,67
*		115	*Maytenus viscifolia* Grisebach		tapia, palta, asperillo, chasqui yuyo, mucamo	134,308,136,413, 281
		116	*Maytenus vitis-idaea* Grisebach		coique-yuyo, carne gorda, sal de indio, palta, yuquí-guaycurú	378,315,413,9, 281
17			CHENOPODIACEAE			
	49	117	*Allenrolfea patagonica* (Moq.)OK.		jume colorado	93,413,379,281
		118	*Allenrolfea vaginata* (Gris.)OK.		jume, jume negro, jume blanco	378,93,315,413, 379,9,281
	50	119	*Atriplex argentina* Spegazzini		cachiyuyo	93,97,281,321
		120	*Atriplex cordobensis* Gaud.& Stuck.		cachiyuyo	413,379,321
		121	*Atriplex eximia* Soriano			321
		122	*Atriplex lampa* (Moquin)Dietrich		cachiyuyo, zampa	9,97,281,321
		123	*Atriplex spegazzinii* Soriano ex Múlg.		cachiyuyo verde, cach. crespo	321
	51	124	*Heterostachys olivaceus* Spegazzini		jumecillo	413, 281

		125	*Heterostachys ritteriana* (Moq.) Ung. Stern		jumecillo	93,413,379,97, 281,157
	52	126	*Holmbergia tweediei* (Moq.) Speg.			93,413,314,97
	53	127	*Salicornia ambigua* Mich.		verdolaga salada	413,281
	54	128	*Suaeda divaricata* Moq.		jume, vidriera	93,315,413,9, 97,281
18			CONVOLVULACEAE			
	55	129	*Ipomoea hieronymi* (OK.) O'Donell			413
		130	*Ipomoea stuckertii* O'Donell			413,379,281
19			ERYTHROXYLACEAE			
	56	131	*Erythroxylum microphyllum* St.-Hil.		tetita de gato	314, h.s.
20			EUPHORBIACEAE			
	57	132	*Acalypha communis* Müll. Arg.		albaquilla, hortensia angosta	413,281,67, h.s.
*		133	*Acalypha poiretti* Spreng.			413,281
	58	134	*Croton bonplandianum* Baill.		tupucharó	413,64
		135	*Croton parvifolius* Müll. Arg.			281
	59		[*Euphorbia* spp.][2]			441
	60	136	*Jatropha chacoana* Fernández Casas			167,179
		137	*Jatropha excisa* Grisebach		higuera del zorro, piñón, sacha higuera, higuerilla, treinta y tres, higuerón, comida del zorro	134,109,308,413, 9,281,159

[2] No woody species are known for the Chaco, where there occur about 12 herbaceous *Euphorbia* species (Subils, 1977)

		138	*Jatropha flavovirens* Pax & K.Hoffm.			159
		139	*Jatropha grossidentata* Pax & K.Hoffm.		piñón	109,379,9
		140	*Jatropha hieronymi* O.Ktze		piñón, sacha higuera	134,308,256
		141	*Jatropha macrocarpa* Grisebach		piñón, sacha higuera, ortigón bravo macho	134,308,315,9, 159, 256
		142	*Jatropha matacensis* Castellanos			109,379
	61	143	*Julocroton subpannosus* Müll. Arg.			413,281
	62	144	*Sapium hæmatospermum* Müll. Arg.		lecherón, curupí	315,413,281
*	63	145	*Sebastiania klotzschiana* (M.A.)M.Arg.		blanquillo, amarillo	134,281
*	64	146	*Stillingia bodenbenderi* (OK.)McVaugh		lechilla	379,281
21			FABACEAE			
			CAESALPINIOIDEAE			
	65	147	*Bauhinia argentinensis* Burkart **var.** *argentinensis*		pata de vaca, pata de buey, ilta´a, wayka amnek	84,178
	66	148	*Caesalpinia gilliesii* Wall. ex Hook.		lagaña de perro, barba de chivo, piscala, espiga de amor, mal de ojos, disciplina de monja, etc.	134,378,84,413, 281
*M		149	*Caesalpinia mimosifolia* Grisebach		pishcalilla	134,84,413
		150	*Caesalpinia paraguariensis* (D.Parodi) Burkart	*C. melanocarpa* Gris.	guayacán, guayacán negro, ibirá-berá	378,84,315,379, 9,97,67
		151	*Caesalpinia stuckertii* Hassler		guaycurú, huay-curú, hai-curú	134,84,379

	67	152	*Cercidium praecox* (R. & Pav.) Harms	*C. australe* Johnston	brea, chañar brea	378,84,315,379, 9,97,281
	68	153	*Lophocarpinia aculeatifolia* (Burkart) Burkart	*Cenostigma* ? *aculeatifolia* Burkart	brea del bordo	84,86,379
	69	154	*Parkinsonia aculeata* L.		cina-cina	84,315,97
	70	155	*Senna acanthoclada* (Gris.) Irwin & Barneby	*Cassia acanthoclada* Gris.		84,413, 379,73, 281
M		156	*Senna aphylla* (Cav.) Irwin & Barneby	*Cassia aphylla* Cav.	pichana, pichanilla, retamilla, cabello de indio, escoba dura	134,378,84,109, 315,413,379,73
		157	*Senna chacöensis* (Bravo) Irwin & Barneby	*Cassia chacöensis* Br.; *C. rigida* (Hier.) Burk. **var.** *robusta* Burkart	palo mataco, timoyuyo, retama, matorral, timo, barba de tigre	84,315,413,73, 281
		158	*Senna chloroclada* (Harms) Irwin & Barneby	*Cassia chloroclada* Harms	sacha-alfa, iauham iaamit [lengua]	84,315,379,9, 74
		159	*Senna morongii* (Britton) Irwin & Barneby	*Cassia morongii* Brit.; *C. rojasiana* Hassler	sen, pito, p. canuto, algarrobo de los caranchos	84,109,413,281, 74
		160	*Senna occidentalis* (L.) Irwin & Barneby	*Cassia occidentalis* L.	café cimarrón, café de Bonpland, taperibá, fedegoso	84,109,413,281, 74
		161	*Senna spiniflora* (Burk.)Irw. & Barneby	*Cassia spiniflora* Burk.		84,73
	71	162	*Stenodrepanum bergii* Harms			84,413,379,281
M	72	163	*Zuccagnia punctata* Cavanilles		pus-pus, jarilla macho, j. pispito	84,379
			MIMOSOIDEAE			

	73	164	*Acacia aroma* Gill. ex Hook. & Arn.	*A. moniliformis* Gris.	tusca, aromita, aromo negro, espinillo Santa Fe	378,84,315,9, 97,281,117,67
		165	*Acacia atramentaria* Benth.	*Prosopis astringens* Gill.	espinillo negro, e.bravo, e.fuerte, aromo negro, garabato negro, etc	84,413,281,117
		166	*Acacia bonariensis* Gill. ex Hook. & Arn.		ñapindá, yuquerí, y. morotí, uña de gato, garabato, g. blanco, etc	84,97,117
		167	*Acacia caven* (Mol.) Mol. var. *caven*	*A. cavenia* (Mol.) H&A.	churqui, aromita, espinillo, e. de bañado, e. Santa Fe, e. flojo, cavén, aromo criollo	378,315,9,117
			var. *dehiscens* Burk. ex Cialdella			379,117
			var. *microcarpa* (Speg.)Burk. ex Ciald.			117
		168	*Acacia curvifructa* Burkart		churqui, tusca gorda	84,117,67
		169	*Acacia furcatispina* Burkart	*A. furcata* Gill. ex Hook. & Arn.	teatín, brea, tintitaco, garabato negro, g. macho, g. rubio, etc.	378,84,315,9, 97,281,117
		170	*Acacia macracantha* Humb. & Bonp. ex Willdenow		tusca, jarro	84,315,379,9, 97,117
		171	*Acacia praecox* Grisebach	*A. hassleri* Chodat	garabato, g.negro, yuquerí negro	378,84,315,117
		172	*Acacia tucumanensis* Grisebach	*A. riparia* auct.	garabato, g. negro, g. blanco	84,315,97,117
*		173	*Acacia visco* Lor. ex Grisebach	*A. polyphylla* Clos	visco, v.negro, arca, viste, viscote	84,379,97,117
	74	174	*Desmanthus brevipes* B.L.Turner	*D. chacoënsis* Burkart		84,87
	75	175	*Mimosa argentinensis* Burkart		vergonzosa	84
		176	*Mimosa detinens* Benth.		sinqui, s. blanco, teatín, garabato, g. blanco	378,84,315,413, 9,97,281,67
		177	*Mimosa farinosa* Grisebach		sinqui, shinque, tusca blanca	84,315,413,9

	76	178	*Mimozyganthus carinatus* (Gris.) Burkart	*Mimosa carinata* Gris.	iscayante, lata, diamante	134,378,84,315, 413,9,97,281
	77	179	*Prosopis* [3] *abbreviata* Bentham		algarrobillo espinoso	134,379,88
		180	*Prosopis affinis* Sprengel	*P. algarobilla* Gris.; *P. nandubey* Lor.ex Gris.	ñandubay, algarrobillo, ibopé-morotí, espinillo	413,97,88
		181	*Prosopis alba* Grisebach **var.** *alba*	*P. atacamensis* Philip.	algarrobo blanco, árbol, á.blanco, ibopé-pará	378,315,379,9, 97,88,281,67
			var. *panta* Gris.	*P. panta* (Gris.)Hieron.	alg. panta, a.impanta, cama tala	134,413,88
*		182	*Prosopis campestris* Grisebach		algarrobito/illo, alpataco chico	134,413,88,281
M		183	*Prosopis chilensis* (Mol.) Stuntz emend. Burkart **var.** *chilensis*	*Ceratonia chilensis* Molina	algarrobo, a. blanco, a. chileno, árbol blanco	134,315,413,88, 281
		184	*Prosopis elata* (Burkart) Burkart	*P.campestris* Gris. **var.** *elata* Burkart	algarrobito, huaschillo, guajchillo, quiscataco	315,413,88,281, 67
		185	*Prosopis fiebrigii* Harms			88
		186	*Prosopis hassleri* Harms **var.** *hassleri*		algarrobo paraguayo, ibopé-hú	134,88,67
			var. *nigroides* Burkart		algarrobo amarillo	88
*		187	*Prosopis humilis* Gill. ex Hook. & Arn.		algarrobilla, barba de tigre	134,413,88,281
		188	*Prosopis kuntzei* Harms	*P.barbatigridis* Stuck.; *P.casadensis* Penzig	palo mataco, jacarandá, barba de tigre, itín, carandá, lanza-lanza	378,315,413,379, 97,88,281,67

[3] A number of natural hybrids between some of the Chaco species of *Prosopis* have been studied by Palacios & Bravo (1981): *P. ruscifolia* x *P. nigra* , *P. ruscifolia* x *P. alba* , *P. ruscifolia* x *P. hassleri* , *P. hassleri* x *P. alba* , *P. hassleri* x *P. fiebrigii* , *P. hassleri* x *P. nigra* , *P. alba* x *P. nigra* , *P. alba* x *P. fiebrigii* , *P. hassleri* x *P. fiebrigii* x *P. alba* .

		189	*Prosopis nigra* (Grisebach)Hieronymus **var.** *nigra*	*P. dulcis* Kunth var. *australis* Bentham	algarrobo negro, yura-tacu, árbol negro, ibopé-hú	378,315,379,9, 97,88,281,67
			var. *ragonesei* Burkart		algarrobo amarillo	413,88
			var. *longispina* Burkart		algarrobillo	88
		190	*Prosopis pugionata* Burkart		algarrobo de las salinas,alpataco	413,379,88,281
		191	*Prosopis reptans* Benth. **var.** *reptans*		mastuerzo, retortuño, retortón	93,413,97,88
		192	*Prosopis rojasiana* Burkart	*P.striata sensu* Fiebrig		88
		193	*Prosopis ruscifolia* Grisebach		vinal, visnal, ibopé-morotí, quilín, algarrobo blanco	378,315,379,315, 97,88,281
		194	*Prosopis sericantha* Gill. ex Hook. & Arn.		barba de tigre, albardón, temoj, retama, huaschilla, timo-yuyo	315,315,413,379, 9,88,281
M		195	*Prosopis torquata* (Cav.ex Lagasca) DC.	*P.adesmioides* Gris.	quenti, tintitaco, schinqui, tusca, lata, ischilín, quintitacu, etc.	378,315,413,97, 88,281
		196	*Prosopis vinalillo* Stuckert		vinalillo, quilín, algarrobo santiagueño	378,315,413,9, 97,88
			PAPILIONOIDEAE			
*	78	197	*Apurimacia dolichocarpa* (Gris.) Burk.	*Tephrosia dolich.* Gris.		84,379,281
*	79	198	*Collaea argentina* Gris.			84,91
	80	199	*Coursetia hassleri* Chodat [4]	*C. guaranitica* Chod.; *Cracca corumbae* Hoeh		281,84, 253, Lavin, *in litt.*

[4] Usually known in the Argentine literature as *Benthamantha glabrescens* (Benth.) Burkart (a combination never legitimately published by Burkart, and in any case superfluous to *B. glabrescens* (Benth.) Alefeld) or *Cracca glabrescens* (Benth.) Benth, all of which are at present synonyms of *C.*

	81	200	*Geoffroea decorticans* (Hook. & Arn.) Burkart	*Gourleia decorticans* Gill. ex Hook. & Arn.	chañar	378,83,315,379, 9,97,281,67
*	82	201	*Psoralea higuerilla* Gill.	*P.higuera* Gris.	higuerilla	84,91
*M	83	202	*Ramorinoa girolae* Spegazzini		chica	84,379
*	84	203	*Sophora linearifolia* Grisebach			84,379,281
22			FLACOURTIACEAE			
*	85	204	*Banara umbraticola* Arechav.			413,281
23			LAMIACEAE			
*	86	205	*Minthostachys mollis* Berg		peperina, poleo	134,97,64
*		206	*Minthostachys verticillata* (Gris.)Epling		peperina	281,453
24			LOBELIACEAE			
*	87	207	*Siphocampylus foliosus* Grisebach			281,91
25			LYTHRACEAE			
	88	208	*Heimia salicifolia* (Kunth) Link		quiebra arado	413,9,97,281
26			MALPIGHIACEAE			
*	89	209	*Cordobia argentea* (Gris.) Niedenzu			336,329,413,281
	90	210	*Janusia guaranitica* (St.-Hil.) Juss.		mariposa, loconte chico	336,329,413,67
*	91	211	*Mionandra camareoides* Grisebach			336
M	92	212	*Tricomaria usillo* (Gill.) Hook.& Arn.		usillo, surí pelado	336,329,413,281

caribaea (Jacq.) Lavin var. *ochroleuca* (Jacq.) Lavin (Lavin, 1988) which reaches neither Argentina nor the Chaco. In Lavin's view (*in litt.*) Fig. 72 in Burkart (1952, p.262) is definitely *C. hassleri* Chod., and in all likelihood this is the taxon generally misidentified for *B. glabrescens* (see Adámoli et al., 1972; Luti et al., 1979).

27			MALVACEAE			
	93	213	*Abutilon virgatum* (Cav.) Sw.			413,7,281
	94	214	*Pavonia argentina* Gürk.			413
	95	215	*Sida argentina* K.Schum.			315,413,281
		216	*Sida dictyocarpa* Grisebach			109,315,9,67
		217	*Sida spinosa* L.			315,281,67, h.s.
	96	218	*Sphaeralcea bonariensis* (Cav.) Gris.		malvisco	109,315,67
		219	*Sphaeralcea miniata* (Cav.) Spach.			97
	97	220	*Wissadula densiflora* R.E.Fries			315,413,281,67
28			MENISPERMACEAE			
	98	221	*Cissampelos pareira* L. **var.** *gardneri* Diels		zarza, caá-pebá, pareira brava, mbaracayá-nambí	134,109,64,228
	99	222	*Odontocarya asarifolia* Barneby			39
		223	*Odontocarya thamnoides* (DC.) Miers		uva del monte	134,64,228
29			MYRTACEAE			
*	100	224	*Myrcianthes cisplatensis* (Camb.) Berg.	*Eugenia cispl.* Camb.	mato, vil-vil, güili, sacha mato	136,413,281
30			NYCTAGINACEAE			
	101	225	*Bougainvillea campanulata* Heimerl.		palo amarillo, guáncar, espuela de gallo, coronillo	134,315,9,451, 67,452
		226	*Bougainvillea infesta* Grisebach		duraznillo	134,315,452,97
		227	*Bougainvillea praecox* Grisebach		duraznillo	134,315,452,97
M		228	*Bougainvillea spinosa* (Cav.) Heimerl.			134,413,452

*M		229	*Bougainvillea stipitata* Grisebach		alfiler/illo, taludo, guáncar falso, talafalsa, coronillo blanco	134,413,451,281, 452
31			OLACACEAE			
	102	230	*Ximenia americana* L.	*Amyris ? arborescens* P. Browne	albaricoque, albarillo del campo, pata, p. del monte, albaría, etc.	134,378,109,413, 281,64,428,67
32			OLEACEAE			
	103	231	*Menodora integrifolia* (Cham. & Schlech.) Steyerm.			413,97,281,64, 228,67
33			POLYGALACEAE			
*	104	232	*Monnina dictyocarpa* Grisebach			413,228
34			POLYGONACEAE			
	105	233	*Ruprechtia apetala* Weddell	*R. corylifolia* Gris.; *R. mollis* Wedd.; *R. boliviensis* Herzog	manzano del campo, higuerón /illa, h. macho/hembra, sacha manzana, duraznillo, d. blanco	378,119,315,120, 413,379,9,97, 281,67
		234	*Ruprechtia triflora* Grisebach	*Triplaris triflora* (Gris.) O. Kuntze	duraznillo colorado, d. blanco, choroqui, guaimí-piré	378,109,119,315, 120,379,9,67
35			PORTULACACEAE			
	106	235	*Amphipetalum paraguayense* Bacig.[5]		initsakás [Manjuy]	41
	107	236	*Grahamia bracteata* Gill. ex Hook. & Arn.		vinagrillo	134,93,413,97, 281,157

[5] This is a herbaceous plant, though with a thick, fleshy root, included here because this recently described genus (Bacigalupo, 1988) is endemic to the Chaco.

36			RANUNCULACEAE			
	108	237	*Clematis montevidensis* Spreng.	*C. hilarii* Spreng.	loconte, bejuco, centella, barba de viejo, zarza, cabello de indio, etc.	134,413,314,281, 453,67
37			RHAMNACEAE			
*M	109	238	*Colletia spinosissima* Gmel.	*C. horrida* Wildenow; *C. spinosa* Lam.	tola, crucero/illo, chacay, barba de tigre, brusquilla, espino negro	134,155,413,97, 281
*	110	239	*Condalia buxifolia* Reissek		piquillín grande, p. negro, p. de la sierra, orta	134,155,136,64
		240	*Condalia microphylla* Cav.	*C. lineata* A.Gray	piquillín, p. rubio	155,378,315,413, 97,281,64
*		241	*Condalia montana* Castellanos		piquillín de la sierra, p. negro	155,413,281
	111	242	*Scutia buxifolia* Reissek	*Adolia bux.* (Reiss.)OK.	coronillo	155,378,234,97
	112	243	*Ziziphus mistol* Grisebach		mistol	155,378,315,413, 9,97,281,67
38			ROSACEAE			
*	113	244	*Kageneckia lanceolata* Ruiz & Pavón		sacha durazno, d. de la sierra	134,413,281,256
39			RUTACEAE			
*	114	245	*Fagara coco* (Gill.) Engler	*Zanthxylum coco* Gill.	coco, coc(h)ucho, sauco hediondo	378,156,413,379
40			SANTALACEAE			
	115	246	*Acanthosyris falcata* (Mart. & Eichler) Grisebach		sacha pera, saucillo, sombra de toro hembra	378,109,315,150, 97

	116	247	*Jodina rhombifolia* Hook. & Arn.	*J. ruscifolia* H.& Arn.; *J. cuneifolia* Miers	sombra de toro, quebracho flojo, peje, chuán, quinchilín	378,315,136,413, 150,97,281
41			SAPINDACEAE			
	117	248	*Allophyllus edulis* (St.-Hil.) Radlk.	*Schmidelia edulis* St.-Hil.	chalchal, koku, picazú-rembiú, coquy, comida de paloma, etc.	134,378,136,9, 7,64
	118	249	*Urvillea uniloba* Radlk.			413,7
42			SAPOTACEAE			
	119	250	*Sideroxylon obtusifolium* (Roem. & Schult.) Pennington **subsp.** *obtusifolium*	*Bumelia obtusifolia* Roem.& Schult.; *B. sartorum* Martius	guaraniná, molle blanco, m. del monte, m.crespo, m.negro, ibirá-niná, horco-molle, chiri-molle	134,378,136,109, 413,314,7,97, 281, 67,351
43			SCROPHULARIACEAE			
*M	120	251	*Monttea schickendantzii* Hieron.		tintillo, olivillo	134,281
44			SIMAROUBACEAE			
	121	252	*Castela coccinea* Grisebach		meloncillo, molle negro, mistol del zorro, quillai, sacha-melón	378,109,315,413, 9,97,281,67
45			SOLANACEAE			
	122	253	*Capsicum chacöense* A.T. Hunziker		ají silvestre	314,281
	123	254	*Cestrum parquii* L'Héritier		duraznillo negro	281
	124	255	*Grabowskia duplicata* Arnott		burro micuna, pata, matorral	315,413,314,97, 281,67
		256	*Grabowskia obtusa* Arnott		burro micuna, matorral, uña de tigre, chil, albaricoque	134,109,315,314

	125	257	*Lycium americanum* Jacquin		chile, chili, yuquyrá menor	314,60
		258	*Lycium athium* Bernardello			60
		259	*Lycium cestroides* Schlechtendal	*Acnistus cestroides* (Schlech.) Miers	comida devíbora, ischivil, chile/i, tala churqui, chivil, talilla, etc.	413,281,60
M		260	*Lycium chilense* Miers ex Bertero **var.** *chilense*	*L. scoparium* Miers; *L. hunzikeri* Barkley	yaoyín, yauyín, coralillo	413,60
M			**var.** *confertifolium* (Miers) Barkley	*L. melanopotamicum* Niederlein		60
M			**var.** *filifolium* (Miers) Bernardello	*L. filifolium* G. ex Ms.	yauyín, frutita de la víbora	60
		261	*Lycium ciliatum* Schlechtendal	*L. argentinum* Hieron.	chivil, comida de víbora, c. burro	315,413,60
		262	*Lycium cuneatum* Dammer	*L.c.* **var.** *rojasii* Barkl.	tala, t.negro, penkoshit, etc.	60
		263	*Lycium elongatum* Miers	*L. confertum* Miers	comida de mula, pinchagua	281,60
		264	*Lycium infaustum* Miers	*L. tweedianum* Gris.	pela surí, chil, tomatillo	413,281,60
		265	*Lycium morongii* Britton	*L.m.***var.***indutum* Hler	pie de calva, yuá, keesiték	60
		266	*Lycium nodosum* Miers		chiguil, yuá chico, fecijciuk	60
M		267	*Lycium tenuispinosum* Miers **var.** *tenuispinosum*	*L. pubescens* Miers; *L. spinulosum* Miers	pela surí, piquillín de las víboras, yauyín espinudo	413,281,60
M			**var.** *friesii* (Dammer) Hitchcock	*L. venturii* Hitchcock	comida de mula, pinchagua	60
	126	268	*Solanum argentinum* Bitt. & Lillo		cabrayuyo, c. negro, afata, hediodilla del monte	315,9,281,67
		269	*Solanum chroniotrichum* Morton		cabrayuyo	h.s.
		270	*Solanum diflorum* Vell.			h.s.

		271	*Solanum glaucophyllum* Desf.	*S.malacoxylon* Sendt.	duraznillo, d. blanco, varilla	314,9,97
	127	272	*Vassobia breviflora* (Sendtner)Hunziker	*Acnistus brev.* Sendt.; *A.parviflorus* Gris.	candelilla, chalchal de gallina, yuá, ischivil, palo negro, etc.	314,229, h.s.
46			STERCULIACEAE			
	128	273	*Ayenia acalyphifolia* Grisebach			128
*		274	*Ayenia cordobensis* (Hieron.) Hieron.			128,281
		275	*Ayenia eliae* Cristóbal			128,67
		276	*Ayenia lingulata* Grisebach			128
		277	*Ayenia o'donellii* Cristóbal			315,128,67
47			ULMACEAE			
	129	278	*Celtis pallida* Torrey **subsp.** *pallida*	*C.spinosa* Spr. **var.** *pallida* (Torr.)Johnston		405,281
			subsp. *sericea* (Romanc.) Rom.& Mart.	*C.sericea* Romanczuk; [*C.chichape*(Wedd)Miq.]	tala negra, t.chica, t.churqui, t.pispa	315,413,97,405
		279	*Celtis spinosa* Sprengel		tala	378,97,405
		280	*Celtis tala* Gill. ex Planchon	*C.sellowiana* Miquel	tala	315,413,97,405
48			VERBENACEAE			
*M	130	281	*Aloysia catamarcensis* Mold.		salvia blanca	68
		282	*Aloysia gratissima* (Gill. & Hook.) Tronc **var.** *gratissima*	*A. lycioides* Cham.; *Lippia lycioides* (Cham.) Steud.	azahar del campo, palo de ángel, poleo del campo, p.chaqueño, niño-rupá chico, cedrón d.monte	134,314,97,281, 68,64,453,67
			var. *angustifolia* (Tronc.) Botta			68

			var. *chacoensis* (Mold.) Botta	*A. chacoensis* Mold.		68
			var. *schulziana* (Mold.) Botta			68
		283	*Aloysia polystachia* (Gris.) Mold.	*Lippia polystachia* Gris	poleo real/de Castilla, té de burro	68,453
*		284	*Aloysia scorodonioides* (Kunth) Cham. **var.** *scorodonioides*			68,67
	131	285	*Lippia integrifolia* (Gris.) Hieron.	*L.turbinata* Gris. **var.***integrifolia* Gris.	poleo, manzanillo, té de inca	134,413,379,281, 453
		286	*Lippia salsa* Grisebach		yerba del ciervo	413,281,157, h.s.
		287	*Lippia turbinata* Grisebach		poleo, té del país	413,7,281
M	132	288	*Xeroaloysia ovatifolia* (Mold.) Tronc.	*Aloysia ovatifolia* Mold.		458,281
49			ZYGOPHYLLACEAE			
	133	289	*Bulnesia bonariensis* Grisebach		guacle, jaboncillo, laca, gluaca, guacho/a, palo flojo	134,378,315,413, 97,281,343,67
		290	*Bulnesia foliosa* Grisebach		palo jabón, jaboncillo, retamo de salinas, r. hojudo	315,413,97,343, 230
M		291	*Bulnesia retama* (Gill. ex H.& A.) Gris.	*B. macrocarpa* Phil.	retamo, retama	413,379,281,343
		292	*Bulnesia sarmientoi* Lorentz ex Gris.	*B. gancedoi* Rojas	palo santo, hok [Mataco], guayacán (Bolivia)	134,378,109,315, 9,97,230,343
M		293	*Bulnesia schickendantzii* Hieron.		rodajillo	379,343
M	134	294	*Larrea cuneifolia* Cav.		jarilla pispa, j.crespa, j.macho, j. del campo	134,378,413,379, 281

M		295	*Larrea divaricata* Cav.		jarilla, j.hembra, j. del cerro	134,378,315,413, 7,281
M	135	296	*Plectrocarpa tetracantha* Gill. ex Hook. & Arn.		rodajillo	413,97,281,157
	136	297	*Porlieria microphylla* (Baill.) Desc., O'Don. & Lourt.		cucharero, palo cuchara, chucupí, guayacán, cuchupí	378,315,413,9, 97,281,67

4.2- Woody and succulent species of the Caatingas :

In the floristic list of woody and succulent species of the Caatingas, those indicated with an asterisk (*) correspond to the more characteristic taxa known to occur in the region, based mainly in Andrade-Lima's works (1954,1960,1970,1981). In the 'Main Synonym' column the names between brackets ([...]) are common identification mistakes or binomials wrongly applied to the entities shown in the 'Species Name' column, not to be treated as taxonomic synonyms. In the 'References' column, h.s. stands for 'herbarium specimens' in those cases in which exsiccata have been taken by the present author as evidence of the alleged presence of the species in the area.

Fly Nº	Gen Nº	Sp Nº	SPECIES NAME	MAIN SYNONYM	VERNACULAR NAME	REFERENCES
1			ANACARDIACEAE			
	1	1	*Astronium concinnum* Schott	*A. macrocalyx* Engler	itapicurú vermelho, i.ferreiro, guaribú, aroeira do Mucury	48,51
*		2	*Astronium urundeuva* (Fr.All.) Engler		aroeira	17,18,29,31,33,168, 170,153,400,180, 51,106,173, 337,36
	2	3	*Loxopterigium gardneri* Engler	*Apterokarpos gardneri* (Engl.) Rizzini	aroeira-mole	46,396,397,51
*	3	4	*Schinopsis brasiliensis* Engler **var.** *brasiliensis*		brauna, baraúna	17,18,29,31,32,168, 34,170,400,180,51, 174,106, 337,36
			var. *glabra* Engler	*S.glabra* (En.)B.&Mey.	brauna, baraúna, b. do norte	304

*	4	5	*Spondias tuberosa* Arruda		imbuzeiro, imbú, umbú, umbuzeiro	12,17,18,28,29,397, 168,170,153,400, 200,51,106, 337,36
2			ANNONACEAE			
	5	6	*Annona spinescens* Mart.		araticum-de-espinho	280,208,34?,51, 106?
		7	*Annona vepertorum* Mart.		bruteiro	280,208,34?,51, 106?
	6	8	*Rolliniopsis leptopetala* (Fries) Safford			208,180
3			APOCYNACEAE			
	7	9	*Allamanda blanchetii* A.DC.		pente-de-mocó, quatro-patacas, sete-patacas, sete-patacas roxa	32?,153?,180,36
		10	*Allamanda martii* Müll. Arg.			36
		11	*Allamanda puberula* DC. **var.** *puberula*		sete-patacas, sete-p. amarela	397,208,153?,36
			var. *glabrata* Müll. Arg.			208
		12	*Allamanda œnotherifolia* Pohl			397,208
	8	13	*Aspidosperma cuspa* (Kunth) Blake		pereiro, p. branco, p. amargo/so	397,153,174,286
		14	*Aspidosperma discolor* A.DC.	*A. francisci* A.DC.	pau-pereiro, peroba, caranaúba	286
*		15	*Aspidosperma polyneuron* Müll. Arg.		amargoso, palo rosa	51,286
		16	*Aspidosperma pyrifolium* Mart.	*A. refractum* Mart.; *A. populifolium* A.DC.	pereiro, pau-pereiro	17,18,33,168,170, 400,180,51,106, 173,337,286,212, 36

		17	*Aspidosperma riedelii* Müll. Arg. **subsp.** *oliganthum* (Wood.) Marc.-Ferr.	*A. oliganthum* Woodson		286
	9	18	*Rauvolfia pauciflora* DC.			208
	10	19	*Skytanthus hancorniaefolius* Mart.			32,208
4			ARALIACEAE			
	11	20	*Pentapanax warmingianus* (Marchal) Harms	*Coemansia w.* March.; *Coudenbergia w.*Marc.	tingui-bravo, salbugueirão	35,51
5			ARECACEAE			
*	12	21	*Copernicia cerifera* (Arr.Cam.) Mart.	*C. prunifera* (Miller) H.E.Moore	carnaúba, carnaubeira	17,18,34,153,51, 173,36
	13	22	*Syagrus comosa* (Mart.) Mart.		catolé	280,195
*		23	*Syagrus coronata* (Mart.) Becc.		ouricuri, licuri	280,18,34,51,195
		24	*Syagrus microphylla* Burret			195
		25	*Syagrus oleracea* (Mart.) Becc.		catolé, coco catolé	180,106,195,36
		26	*Syagrus vagans* (Bondar) Hawkes		ariri, licurioba	195
		27	*Syagrus wedermannii* Burret		coco da vassoura	195
		28	*Syagrus* x *matafome* (Bondar) Glassm.		matafome, coco matafome	51,195
6			ASTERACEAE			
	14	29	*Blanchetia heterotricha* DC.			208
	15	30	*Dasyphyllum candolleanum* (Gardner) Cabrera	*Flotovia candolleana* Gardner		94
	16	31	*Eremanthus martii* Baker		chico-Rodrigo	280,208,153

	17	32	*Lagascea mollis* Cav.			440,208
	18	33	*Pectis decumbens* (Gard.) Sch.Bip.			52
		34	*Pectis elongata* Kunth		cuminho-bravo, alecrim, etc.	52
		35	*Pectis linifolia* L. **var.** *linifolia*			52
	19	36	*Telmatophila scolymastrum* Mart. ex Baker		carrapicho-de-lagoa	36
	20	37	*Wunderlichia crulsiana* Taub.			280
7			BIGNONIACEAE			
	21	38	*Anemopægna velutinum* Mart. ex DC.			208, h.s.
	22	39	*Arrabidea chica* (Humb.& Bonpl.) Verl.		cipó preta da serra	337
		40	*Arrabidea corallina* (Jacq.) Sandwith	*Bignonia cor.* Jacq.; *A. rhodantha* Bur.& Sch.	cipó açoita cavalo	337
	23	41	*Cuspidaria argentea* (Wawra) Sandw.			208
	24	42	*Godmania dardanoi* (J.C.Gomes) Gentry	*Xerotecoma dardanoi* J.C.Gomes	umbigo-de-viúva, chifre-de-carneiro	28,397,188,35,51, 36
	25	43	*Jacaranda irwinii* A.H. Gentry			306
		44	*Jacaranda jasminoides* (Thunb.) Sand.			208,306
	26	45	*Pyrostegia venusta* (Ker.) Miers			280,337
*	27	46	*Tabebuia aurea* (Manso) ? [Gentry, *in litt.*]	*T.caraiba* (Mart.) Bur.	craibeira, caraibeira, paratudo	17,18,28,168,170, 400,51,106,36

*		47	*Tabebuia impetiginosa* (Mart. ex DC.) Standley	*T.avellanedae* Lorentz ex Griseb.;*T.ipe* (Mart. ex Schum.) Standley	pau d'arco roxo	31,32,34,153,180, 51,173,337
		48	*Tabebuia roseo-alba* (Ridley) Sandwith		paudarquinho	32, Proença (pers.comm.)
		49	*Tabebuia spongiosa* Rizzini		sete-cascas, cascudo	397,153,180,106, 36
8			BOMBACACEAE			
*	28	50	*Cavanillesia arborea* Schum.		barriguda, b. lisa, embaré, imbaré	283,31,32,168,34, 51,360,36
*	29	51	*Ceiba glaziovii* (Kuntze) Schum.	*Chorisia gl.* (K.)Sant.; [*Ceiba erianthos* Sch.]	barriguda	17,283,31,168,34, 180?,51,360,36
	30	52	*Eriotheca parvifolia* (Mart.& Zucc.) Robyns	*Bombax parvifolium* Mart.& Zucc.	embiratanha?	399,22?,173,337?
*	31	53	*Pseudobombax simplicifolium* Robyns		embiratanha, imbiratanha, imbiraçu, imbiruçu, imburuçu	399,29?,397,32, 170,153,51,106,36
9			BORAGINACEAE			
	32	54	*Auxemma glazioviana* Taub.		pau-branco, folha larga	22,397,51,173
*		55	*Auxemma oncocalyx* (Fr.All.) Taub.		pau-branco, frei-jorge	22,33,34,51,173, 36
	33	56	*Cordia curassavica* (J.) Roem.&Schult.			445
		57	*Cordia dardani* Taroda			445
		58	*Cordia globosa* (Jacq.) Kunth		moleque-duro branco/pequeno	180,445,106,282
		59	*Cordia insignis* Cham.		folha larga	397,32,180,51,446

*		60	*Cordia leucocephala* Moricand		moleque-duro, m.-d. preto, m.-d. grande, negro-duro	17,33,168,34,170, 153,171,180,200, 445,106,337,36, 282
*		61	*Cordia trichotoma* (Vell.) Arrab. ex Steud.	[complex with *C. alliodora* (R.&P.) Oken]	freijorge, claraiba, freijó, cabo-de-machado	138,32,153,193, 174,51,173,446, 337
	34	62	*Patagonula bahiensis* Moricand		mulambá	397,208,51, h.s.
	35	63	*Tournefortia rubicunda* Salzm. ex DC.			208
10			BROMELIACEAE			
	36	64	*Aechmea aquilega* (Salisbury) Gris. **var.** *chrysocoma* (Baker) L.B. Smith	*A.chrysocoma* Baker; *Hohenbergia c.* Baker	croatá	432
		65	*Aechmea eurycorymbus* Harms			432
		66	*Aechmea lingulata* (L.) Baker **var.** *lingulata*	*Hohenbergia odora* (Mq)Bak;*Bromelia l.* L.	gravatá	432
	37	67	*Billbergia porteana* Brongniart ex Beer			280,432,400
*	38	68	*Bromelia laciniosa* Mart. ex Schult.		macambira, macambira-de-cachorro	17,18,26,168,170, 153,200,106,36
	39	69	*Cottendorfia florida* Schultes f.			280,432
	40	70	*Dyckia dissitiflora* Schultes			432
		71	*Dyckia limae* L.B. Smith			432
		72	*Dyckia pernambucana* L.B. Smith			432
*	41	73	*Encholirium spectabile* Mart. ex Schult.		macambira-de-boi, m.-de-lajedo (lageiro), m.-de-flecha/pedra	138,26,32,432,212, 36

	42	74	*Hohenbergia caatingae* Ule		gravatá	26,34,200
*	43	75	*Neoglaziovia variegata* Mez		caroá, crauá	17,18,26,32,168, 170,153,200,180, 106
	44	76	*Pitcairnia flammea* Lindl. **var.** *floccosa* L.B. Smith	*P. muscosa* Mart. ex Schult. f.		280,432
11			BURSERACEAE			
*	45	77	*Commiphora leptophloeos* (Mart.) Gillet	*Bursera leptophloeos* Mart.	imburana, imburana vermelha, imburana de cambão, imburana de espinho	17,18,22,29,31,397, 32,33,194,168,34, 29,153,51
12			CACTACEAE			
	46	78	*Acanthocereus ? albicaulis* Br. & Rose			280,24,90
		79	*Acanthocereus brasiliensis* Br. & Rose			76,90
	47	80	*Arrojadoa penicillata* (Gürke)Br.& Rose		rabo de raposa	36
		81	*Arrojadoa rhodantha* (Gürke)Br.& Rose		rabo de raposa, rabo de onça	280,24,90,400, 106
	48	82	*Austrocephalocereus dybowskii* (Gosselin) Backeberg	*Cephalocereus dybowskii* (Goss.)Br&R	cabeça branca, cabeça-de-velho, mandacarú de penacho	76,36
		83	*Austrocephalocereus purpureus* (Gürke) Backeberg	*Cephalocereus purpureus* Gürke	mandacarú falso	76,32
	49	84	*Brasiliopuntia bahiensis* (Britt. & Rose) Berger	*Opuntia bahiensis* Br.& Rose	palminha, quipá, rumbeba, mumbeca, mumbeba	280,17,24,90, 28, 168

*	50	85	*Cereus jamacaru* P.DC. non SD. ex Pfeiffer		mandacarú, cardeiro	17,18,29,31,168, 170,153,180,51, 106,173,337,36
	51	86	*Discocactus bahiensis* Britt. & Rose			76,90
		87	*Discocactus placentiformis* (Leh.) Sch.			76,90
		88	*Discocactus zehntneri* Britt. & Rose			76,90
	52	89	*Eriocereus adscendens* (Gürke) Berger	*Harrisia adscendens* (Gürke) Britt. & Rose	rabo de raposa, chegue-pra-lá	280,17,24,90,168, 180,106,36
	53	90	*Espostoa ulei* (Gürke) Buxbaum	*Facheiroa ulei* (Gür.) Wer.;*F.pubiflora* Br&R	facheiro	90,71
	54	91	*Leocereus bahiensis* Britt. & Rose		rabo de raposa	76
*	55	92	*Melocactus bahiensis* Britt. & Rose		coroa-de-frade, croa-de-frade, cabeça-de-frade	76,280,17,24,168, 34,170,153,106
		93	*Melocactus horridus* Werdermann		coroa-de-frade	24,259
		94	*Melocactus oreas* Miquel		coroa-de-frade, croa-de-frade	76,24,36
		95	*Melocactus zehntneri* (Br.& Rose) Back.		coroa-de-frade	76,280,24,32
	56	96	*Micranthocereus polyanthus* (Wer)Back			90
*	57	97	*Opuntia inamoena* K.Schum.		quipá, quipá liso	280,17,18,24,168, 170,153,106,36
		98	*Opuntia palmadora* Britt. & Rose		palmatoria, p. brava, quipá, palminha	280,24,168,34,170, 106,36
	58	99	*Pereskia aureiflora* Ritter		facho, ora pro nobis da mata	260

		100	*Pereskia bahiensis* Gürke		quiabento, inh(i)abento, flor de cêra, espinha de Sto Antônio	76,260,36
		101	*Pereskia stenantha* Ritter		quiabento, flor de cêra, espinha de Santo Antônio	260
	59	102	*Pilosocereus catingicola* (Gür.)B.& Row.			76
		103	*Pilosocereus chrysostele* (Vaup.) Byl. & Rowl.	*Pilocereus c.*(Vp.)Werd	facheiro da serra	280,24
		104	*Pilosocereus glaucescens* (Lab.) Byl.& Rowl.		facheiro, facheiro azul	76,400,180,106,36
*		105	*Pilosocereus gounellei* (Web.) Byl. & Rowl.	*Pilocereus gounellei* Web.; *Cereus gounellei* K.Sch.	xique-xique, alastrado	280,17,18,24,168, 34,170,153,400, 180,106,337,36
*		106	*Pilosocereus piauhiensis* (Gürke) Byl. & Rowl.	*Pilocereus p.*(Gür.) Wer.; *Cephalocereus p.* (Gürke.) Br. & Rose	facheiro	280,24,33,168,34, 170?,400,51,36
*		107	*Pilosocereus tuberculatus* (Werd.)Byl.& Rowl.	*Pilocereus tuberculatus* Werd.	caxacubri	17,18,24,34,400
		108	*Pilosocereus zehntneri* (Br.& R.)Byl.& Rowl.	*Cephalocereus zehntneri* Br.& Rose	xique-xique das pedras	76
	60	109	*Quiabentia zehntneri* (Br.& R.)Br.&Rose	*Pereskia z.* Br. & Rose	quiabençio, quiabento	108,90,32
	61	110	*Stephanocereus leucostele* (Gürke) Berger	*Cephalocereus leucostele* (Gür.) B&R		90

	62	111	*Tacinga atropurpurea* Werdermann **var.** *atropurpurea*			161
			var. *zehntnerioides* Backeberg			161
		112	*Tacinga braunii* Esteves			161
		113	*Tacinga funalis* Britton & Rose		quipá voador	76,280,24,90,36
*	63	114	*Zehntenerella squamulosa* Britton & Rose [*Facheiroa squamosa* (Gür.)Br. & Esteves]	*Cereus squamosus* Gürke; *Leocereus sq.* (Gür.)Werd.	facheiro-preta, facheiro	280,90,32,168,34, 173,261,71,337
13			CAPPARIDACEAE			
	64	115	*Capparis flexuosa* L. (*sensu lato*)	[*C.cynophallophora* L.]	feijão-bravo, feijão-de-boi	168,180,174,51, 106,337,282, h.s.
*		116	*Capparis jacobinae* Moric. ex Eichler	*Colicodendron jacobinae* (Mor.) Hut.	icó-prêto, icó-de-cavalo	17,18,397,168,180, 200,51,36
*		117	*Capparis yco* Mart.	*Colicodendron yco* (Mart.) Hutchinson	icó-branco, icó	280,17,18,397,168, 200,106,36
	65	118	*Crateva tapia* L.		trapiá	138,415,153,51
	66	119	*Haptocarpum bahiense* Ule			349
14			CARICACEAE			
	67	120	*Carica quercifolia* (St.-Hil.) Hieron.		mamaozinho	43
	68	121	*Jacaratia spinosa* (Aublet) A.DC.	*J.dodecaphylla* A.DC.	jacaratiá	140,43
		122	*Jacaratia* sp.	[*J.corumbensis* Kuntze?]	mamaozinho, mamaozinho de veado, mamão de veado	32,34,153,400,51, 106

15			CELASTRACEAE			
*	69	123	*Fraunhoffera multiflora* Mart.		pau-branco	17,397,33,34,153, 180,51,106,36
*	70	124	*Maytenus rigida* Mart.		bon-nome, bonomeiro, casca-grossa, pau-de-colher	17,18,32,168,170, 174,51,173,337,36
16			CHRYSOBALANACEAE			
	71	125	*Couepia uiti* (Mart. & Zucc.) Benth.		assicí	280,368,397,208
*	72	126	*Licania rigida* Bentham	[*L.sclerophylla* (Mart. ex Hook.f) Fritsch]	oiticica	12,22,415,368,168, 34,51,337,36
17			COCHLOSPERMACEAE			
	73	127	*Cochlospermum vitifolium* (Willd.) Spreng.	[*C.regium* (Schr.)Pilg.; *C.insigne* St.-Hil.]	algodão bravo, a.do mato, a.-de-veado, pacoté, maria-mole(?)	138,280,32,364, 153,51,173
18			COMBRETACEAE			
	74	128	*Combretum fruticosum* (Loefl.) Stuntz			163
		129	*Combretum lanceolatum* Pohl ex Eichl.			280,163
		130	*Combretum laxum* Jacq.	*C.obtusifolium* Rich.		280,163
*		131	*Combretum leprosum* Martius		mofumbo,vaqueta, vaquetinha	280,22,31,168,170, 153,174,173, 337,36
		132	*Combretum mellifluum* Eichler			280,163
		133	*Combretum monetaria* Martius		cipaúba	163,397
		134	*Combretum pisonioides* Taub.			163
		135	*Combretum rupicola* Ridl.			163

	75	136	*Terminalia fagifolia* Mart. & Zucc.		catinga-de-porco	280,397,208,51
	76	137	*Thiloa glaucocarpa* (Mart.) Eichl.		sipaúba, vaqueiro	138,12,51,106,173
19			CONVOLVULACEAE			
	77	138	*Ipomoea asarifolia* (Desr.)R.& Schult.		salsa, rama-de-peba	208,106
		139	*Ipomoea carnea* Jacq. **subsp.** *fistulosa* (Mart. ex Choisy) D. Austin	*I. fistulosa* Mart. ex Choisy	matacabra	17,18,415, h.s.
20			ERYTHROXYLACEAE			
	78	140	*Erythroxylum betulaceum* Mart.	*E.rosuliferum* Schulz ?	rompe-gibão grande	280,418,106,360
		141	*Erythroxylum bezerrae* Plowman			360,359
		142	*Erythroxylum caatingae* Plowman		imbuzeiro bravo	360
		143	*Erythroxylum campestre* St.-Hil.			280,418
		144	*Erythroxylum flaccidum* Salzman			280,418
		145	*Erythroxylum macrochaetum* Miq.			280,418,360
		146	*Erythroxylum maracasense* Plowman			360
		147	*Erythroxylum nummularia* Peyritsch		rompe-gibão pequeno	280,418,400,180, 106
		148	*Erythroxylum oxypetalum* O.E. Schulz			208,360
		149	*Erythroxylum pelleterianum* St.-Hil.			280,418,360
		150	*Erythroxylum petrae-caballi* Plowman			360
		151	*Erythroxylum polygonoides* Mart.			418,360
		152	*Erythroxylum pungens* O.E. Schulz		rompe-gibão	280,418,397,360, 337

		153	*Erythroxylum revolutum* Mart.		rompe-gibão	280,418,435
		154	*Erythroxylum subrotundum* St.-Hil.			418,400,360
21			EUPHORBIACEAE			
	79	155	*Alchornea castaneaefolia* (Willd.) Juss.		pau-mole	280,17
	80	156	*Cnidoscolus bahianus* (Ule) Pax & Hoff.		favela-de-galhina,orelha-de-onça	346,180,106,36
*		157	*Cnidoscolus phyllacanthus* (Müll.Arg.) Pax & Hoffm.		favela, faveleira, favela de cachorro	280,17,18,168,34, 153,51,106,173,337
		158	*Cnidoscolus vitifolius* Mill. ex Pohl **var.** *obtusifolia* Müll.Arg.		favela brava, cansanção, cansanção-de-vaqueiro	280,346,153,400, 200
*	81	159	*Croton argyrophylloides* Müll.Arg.		marmeleiro da serra, m.branco, vassourinha, sacatinga, velame	280,208,153,180, 174,61,106,337,36
		160	*Croton campestris* St.-Hil.em.Müll.Ar.		marmeleiro, velame	168,153,36
		161	*Croton hemiargyreus* Müll.Arg.		marmeleiro	397,61
		162	*Croton jacobinensis* Baill.		marmeleiro branco	288,81,61,173
		163	*Croton micans* Sw. emend. Müll.Arg.			208
*		164	*Croton sincorensis* Mart.		marmeleiro, marmeleiro branco	17,168,61
*		165	*Croton sonderianus* Müll.Arg.		marmeleiro, marmeleiro preto	170,153,180,174,61 106,173,337, 212,36
		166	*Croton tricolor* Müll.Arg.			208
		167	*Croton zehntneri* Pax & Hoffm.		quebra-faca, canelinha	280,174,337
	82	168	*Ditaxis desertorum* (Müll.Arg.)Pax & Hoffm.	*Argythamnia desertorum* Müll.Arg.		347

		169	*Ditaxis malpighiacea* (Ule) Pax & Hoff.	*Argythamnia mal.* Ule	pau-de-mocó	347,208,400,106
*	83	170	*Euphorbia phosphorea* Mart.		pau-de-leite, barbasco, cumanan, pau-de-camaná	280,17,32,168,34, 173,36
	84	171	*Jatropha mutabilis* (Pohl) Baill.		pinhão, pinhão miúdo	346,208,173,36
*		172	*Jatropha pohliana* Müll.Arg.		pinhão bravo	280,18,397,168,34, 170,153,180,200, 106, 173,212,36
		173	*Jatropha ribifolia* (Pohl) Baill.		pinhão, pinhão pequeno	280,346,208,106, 36
*		174	*Jatropha urens* L.	*Cnidoscolus u.*(L.)Art.	cansanção, urtiga branca	17,32,168,208,153
	85	175	*Manihot brachyandra* Pax & Hoffm.			280,402
		176	*Manihot cærulescens* Pohl emend. Rogers & Appan **subsp.** *cærulescens*	*M. piauhyensis* Ule	maniçoba brava, maniçoba-de-veado	28,402
		177	*Manihot catingae* Ule		maniçoba brava	280,402
		178	*Manihot dichotoma* Ule			280,402
		179	*Manihot epruinosa* Pax & Hoffm.			280,402
*		180	*Manihot glaziovii* Müll.Arg.		maniçoba , maniçobeira, caucho	138,402,168,173, 36
		181	*Manihot heptaphylla* Ule			280,402
		182	*Manihot maracasensis* Ule		maniçoba	280,402
		183	*Manihot pseudoglaziovii* Pax & Hoffm.		maniçoba brava	280,402,106
	86	184	*Maprounea brasiliensis* St.-Hil.			348
		185	*Maprounea guyanensis* Aubl.		pau de leite	348,180,106,337
	87	186	*Sapium argutum* (Müll.Arg.)Huber			348,233

		187	*Sapium cicatricosum* Pax & Hoffm.			348,233
		188	*Sapium montevidense* Klotzch ex Baill.		burra leiteira	348,208,170?, 106?
		189	*Sapium obovatum* Klotzch ex Müll.Arg.			348,208
		190	*Sapium sceleratum* Ridley			348,233
	88	191	*Sebastiania catingae* Ule			348
22			FABACEAE			
			CAESALPINIOIDEAE			
	89	192	*Bauhinia acuruana* Moric.		miroró	262
		193	*Bauhinia cacovia* Wund. **subsp.** *blanchetiana* Wund. ined.			262
		194	*Bauhinia catingae* Harms			262
*		195	*Bauhinia cheilantha* (Bong.) Steud.	*Pauletia cheilantha* Bong.	mororó, mororó preto, miroró	397,34,170,153,180 106,173,262, 337,36
		196	*Bauhinia dumosa* Benth.			262
		197	*Bauhinia estivana* Wund. ined.			262
		198	*Bauhinia flexuosa* Moric.	*Schnella fl.* (M.)Walp.	guela-de-velho, cipó-de-mixla	262, h.s.
		199	*Bauhinia forficata* Link	*B. candicans* Benth.	mão (unha)-de-vaca, miroró	262
		200	*Bauhinia microstachya* (Raddi) Macbr.	*B.bahiensis* Bong.; *B. langsdorffiana* Bong.		262
*		201	*Bauhinia pentandra* (Bong.) Vog. ex Steud.	*B. heterandra* Benth.; *Pauletia pent.* Bong.	mororó, unha-de-vaca, capa bode	17,18,28,51,262

*	90	202	*Caesalpinia bracteosa* Tul.		catingueira, pau-de-rato, pau-santo	33,34,153,174,51, 262,337,36
		203	*Caesalpinia calycina* Benth.			262
*		204	*Caesalpinia ferrea* Mart. ex Tul. **var.** *ferrea*	*C.f.* **var.** *cearensis* Huber	pau ferro	262
			var. *glabrescens* Benth.			262
			var. *parvifolia* Benth.	[*C. leiostachya* (Benth.) Ducke]	pau ferro, jucá	280,17,283,28,397, 170,153,180,51,106 173,262,337, 36,282
		205	*Caesalpinia gardneriana* Benth.			262
		206	*Caesalpinia laxiflora* Tul.			397,262
*		207	*Caesalpinia microphylla* Mart. ex Tul.		catingueira rastreira, c.de porco, arranca-estribo, catinga de porco	280,17,18,397,168, 153,200,106,262, 36
*		208	*Caesalpinia pyramidalis* Tul.		catingueira, catinga de porco, pau-de-rato, mussitáiba	280,17,18,22,397, 168,170,180,51,106 173,262,212, 36,282
*	91	209	*Cenostigma gardnerianum* Tul.	*C.angustifolium* Tul.	caneleiro, canela de velho	33,153,51,262
		210	*Cenostigma macrophyllum* Tul.			262
	92	211	*Chamaecrista acosmifolia* (Benth.) Irwin & Barneby **var.** *acosmifolia*	*Cassia acosmifolia* Benth.		262
		212	*Chamaecrista amiciella* (I&B)Ir.& Bar.	*Cassia amic.* Ir.&Bar.		262

		213	*Chamaecrista barbata* (Nees & Mart.) Irwin & Barneby	*Cassia barbata* Nees & Mart.		262
		214	*Chamaecrista belemii* (I.& B.)Ir.& Bar.	*Cassia belemii* I.& Bar.	flor-de-São João	262
		215	*Chamaecrista carobinha* (I&B)Ir.&Bar.	*Cassia carob.* Ir.&Br.		262
		216	*Chamaecrista desvauxii* (Coll.) Killip **var.** *latifolia* (Benth.) Irwin & Barneby	*Cassia uniflora* Mill. **var.** *latif.* Bth.; *Cassia piauhiensis* Irwin		262
		217	*Chamaecrista pascuorum* (Bth.) I.& B.	*Cassia pascuor.* Benth.		262
		218	*Chamaecrista rotundifolia* (Pers.) Greene **var.** *rotundifolia*	*Cassia rotundifolia* Persoon	pasto-rasteiro	280,262
		219	*Chamaecrista supplex* (Benth.) Br.& R.	*Cassia supplex* Benth.	cabeleira	174,262
		220	*Chamaecrista zygophylloides* (Taub.) Irwin & Barneby	*Cassia zygophylloides* Taub.		280,262
	93	221	*Copaifera coriacea* Mart.	*C.cordifolia* Hayne	copaiv(b)a branca, pau d'óleo	144,51,262
		222	*Copaifera langsdorffii* Desf.	*C.grandiflora* (Benth.) Malme;*C.nitida* Hayne	pau d'óleo do sertão, copaiba vermelha	280,144,180,154, 51,262
		223	*Copaifera luetzelburgii* Harms			144
		224	*Copaifera martii* Hayne	*C. rigida* Benth.	pau d'óleo, jatobá	144,262
	94	225	*Diptychandra aurantiaca* Tul. **subsp.** *epunctata* (Tul.) Lima, Carv. & Costa	*D. epunctata* Tul.	birro branco, biró	397,153,51,262
	95	226	*Goniorrhachis marginata* Taub.		itapicurú, itapicurú preto	397,32,35,51,262
	96	227	*Hymenaea courbaril* L. **var.** *courbaril*		jatobá	18,51

			var. *stilbocarpa* (Hayne) Lee & Lang.	*H. stilbocarpa* Hayne	jatobá de caatinga, jatobá-sertão	262
		228	*Hymenaea eriogyne* Benth.		jatobá	255,51,262
		229	*Hymenaea martiana* Hayne	*H. sellowiana* Hayne	jatobá	280,255,200,262
		230	*Hymenaea velutina* Ducke		jatobá de caatinga,jatobázinho	255,262
	97	231	*Martiodendron mediterraneum* (Mart. ex Benth.) Koeppen	*Martia parvifolia* (Bth.) Benth.; *Martiusia parvifolia* Benth.		244,262
*	98	232	*Parkinsonia aculeata* L.		turco, sensitivo	280,17,18,29,33, 51,262,36
	99	233	*Peltogyne pauciflora* Benth.	*P.glaziovii* (Taub.)Dwy. *Cynometra glaz.* Taub.	buranhe, imburanhe, jitaí	397,400,200,51, 262
	100	234	*Peltophorum dubium* (Spreng.) Taub.	*Caesalpinia dubia* Spr. *P. vogelianum* Benth.	imbira-puitá, farinha seca, canafístula	17,32,262, h.s.
*	101	235	*Poeppigia procera* Presl. **var.** *conferta* Benth.		muquém, sabonete, lava-cabelo, pau-branco, caracu	280,17,18,397,153, 51,262
*	102	236	*Pterogyne nitens* Tul.		madeira nova, amendoim bravo, vilão, sucupira, vassourinha	31,62,34,174,51, 262,36
*	103	237	*Senna acuruensis* (Benth.) Ir. & Barn. **var.** *acuruensis*	*Cassia acuruensis* Benth.	São João, monzê-branco, pau-de-besouro	34,200,262
			var. *catingae* (Harms) Ir. & Barn.	*Cassia catingae* Harms		262
			var. *interjecta* Irwin & Barneby			262
		238	*Senna aversiflora* (Herbert)Ir. & Barn.	*Cassia aversiflora* Her.		262

		239	*Senna gardneri* (Benth.)Ir. & Barneby	*Cassia gardneri* Bent.		280,262
		240	*Senna harleyi* Irwin & Barneby			262
		241	*Senna macranthera* (Coll.) Ir. & Barn. **var.** *pudibunda* (Benth.) Ir. & Barneby	*Cassia macr.* DCexCol. *C.pudibunda* Bth	velame, canafístula da serra	174,262,337
		242	*Senna martiana* (Benth.) Ir. & Barneby	*Cassia martiana* Bth.	mata-pasto, besouro,canafístula	280,397,114,262, 36
		243	*Senna rizzinii* Irwin & Barneby	*Cassia granulata* Rizz.	São João	106,262
*		244	*Senna spectabilis* (DC.) Ir. & Barneby **var.** *excelsa* (Schrader) Ir. & Barn.	*Cassia spectabilis* DC.; *C. excelsa* Schr.; *C.carnaval* Spegazzini	canafístula, c.-de-besouro, São João, pau-de-besouro	280,17,18,28,33, 153,180,51,106, 262,337,36,282
		245	*Senna splendida* (Vog.) Ir. & Barneby **var.** *gloriosa* Irwin & Barneby	*Cassia splendida* Vog.		280,262
		246	*Senna uniflora* (P.Mill.)Ir. & Barneby	*Cassia uniflora* P.Mill.	mata-pasto	168,174,262
			MIMOSOIDEAE			
*	104	247	*Acacia bahiensis* Benth.	*A. tavaresorum* Rizzini	jurema branca, espinheiro, pau-de-fuso,unha de gato, coração de mulato	28,208,34,51,262, 36
		248	*Acacia farnesiana* (L.) Willd.		arapiraca, vinhático-de-espinho	280,394,170,153, 262
		249	*Acacia glomerosa* Benth.		braúna-mongo, maracaípe, etc.	280,394,262,337
		250	*Acacia langsdorffii* Benth.		jurema-unha-de-gato	208,153,262
		251	*Acacia martii* Benth.		espinheiro branco	280,262
		252	*Acacia monacantha* Willd.	*A. velutina* Benth.		117,262

*		253	*Acacia piauhiensis* Benth.		jurema branca, espinheiro, rama-de-boi	280,397,174,106, 262
		254	*Acacia polyphylla* DC.		espinheiro	262
		255	*Acacia riparia* Kunth		unha-de-gato	394,262
	105	256	*Albizia blanchetii* (Benth.) Lewis	*Pithecellobium blanchetii* (Bth.) Benth.	canzil, canela-de-burro, saia-de-comadre	51,262
*		257	*Albizia polyantha* (Spreng.f.) Lewis	*Cathormion polyanthum* (Spr.)Bk.; *Pithecellobium multiflorum*(Kth)Benth	canafístula, muquêm, munzê, canafistula-de-boi	280,17,18,31,397, 34,51,262,36
		258	*Albizia polycephala* (Benth.) Killip	*Pithecellobium polycephalum* Benth.	monzê, camunzê, camondongo, candieiro	17,51,262
*	106	259	*Anadenanthera colubrina* (Vell.) Bren. **var.** *cebil* (Griseb.) Altschul	*Piptadenia macrocarpa* Benth.; *P.m.* **var.** *cebil* (Gris.)Ch.&Hassl.; *A. macrocarpa*(Bent.)Br.	angico, angico-preto, angico-jacaré, angico-vermelho, angico-de-casca, angico-manso, angico-de-umbigo	17,18,11,31,32, 168,34,170,153, 180,200,51,106, 173,262,337,36
*	107	260	*Calliandra depauperata* Benth.		carqueja, carqueijo, alecrim, umari-bravo	18,34,153,174,106, 173,262,337,36
		261	*Calliandra leptopoda* Benth.			280,262,36
		262	*Calliandra macrocalyx* Harms	*C. villosiflora* Harms		397,262
		263	*Calliandra squarrosa* Benth.	*C. catingae* Harms		262

	108	264	*Chloroleucon dumosum* (Benth.) Lewis	*Pithecollobium dumosum* Benth.	arapiraca, pau-rósea, muleque-duro criadinho, coronha (?)	280,153,200,51, 262
*		265	*Chloroleucon foliolosum* (Benth.) Lewis	*Pithecollobium foliolos.* Benth.; *Calliandra aristulata* Rizzini	arapiraca, jurema branca	397,170,180,174, 51,173,262,337, 212
		266	*Chloroleucon mangense* (Jacq.) Britton & Rose	*Pithecollobium mangense* (J.)Mcbr.;*P. parvifolium* (S.)Benth.; *P.oliganthum* Rizz.	arapiraca	29,180,51,106,262
	109	267	*Desmanthus virgatus* Willd.	*Mimosa virgata* L.	jureminha, pena-de-saracura	170,153,262
*	110	268	*Enterolobium contortisiliquum* (Vell.) Morong	*E. timbouva* Mart.; *Mimosa cont.* Vellozo	timbauva, orelha de macaco, tamboril do campo, tamboril	12,17,283,31,180, 51,262
	111	269	*Mimosa acutistipula* Benth.		jurema preta, jureminha	397,174,262
		270	*Mimosa adenophylla* Harms **var.***armandiana* (Rizzini) Barneby			49,262
			var. *mitis* Barneby			49,262
*		271	*Mimosa arenosa* (Willd.) Poir.	*M. malacocentra* (Mart.) Benth.	calumbí, jurema, jurema vermelha, avoador	280,34,174,106, 173,262,337,36
		272	*Mimosa campicola* Harms **var.***planipes* Barneby			49,262
*		273	*Mimosa cæsalpiniifolia* Benth.		sabiá	280,22,33,168,174, 51,173,337,36

		274	*Mimosa coruscocæsia* Barneby			49,262
		275	*Mimosa exalbescens* Barneby			49,262
		276	*Mimosa gemmulata* Barn. **var.***gemmulata*			49,262
		277	*Mimosa glaucula* Barneby			49,262
		278	*Mimosa hexandra* Micheli	*M. fascifolia* Rizz.; *M. acanthophora* Harms	carquejo	397,262
		279	*Mimosa invisa* Mart. ex Colla	*M.rhodostachya* Benth.	calumbí-miúdo	114,262
		280	*Mimosa irrigua* Barneby			49,262
		281	*Mimosa misera* Benth.	*M.franciscana* Benth.; *M.remansoana* Harms		280,262
		282	*Mimosa modesta* Mart.	*M. ursinoides* Harms	malícia	280,262
		283	*Mimosa morroënsis* Barneby			49,262
		284	*Mimosa nothopteris* Barneby			49,262
*		285	*Mimosa ophthalmocentra* Mart.ex Bth.		calumbí-vermelho	280,51,262
		286	*Mimosa paludosa* Benth.			280,262
		287	*Mimosa pigra* L.		calumbí, jiquiri-grande	17,262
		288	*Mimosa pseudosepiaria* Harms		espinheiro bravo	280,262
*		289	*Mimosa tenuiflora* (Willd.) Poir.	*M.hostilis* Benth.; *M. limana* Rizzini	calumbí, jurema preta, espinheiro	280,17,18,28,397, 168,170,180,51,106 173,337,212,36
		290	*Mimosa ulbrichiana* Harms			280,262

		291	*Mimosa ursina* Mart.			262
*		292	*Mimosa verrucosa* Benth.		jurema, jurema rosada	280,397,34,262,36
		293	*Mimosa xiquexiquensis* Barneby sp. nov. ined.			262
	112	294	*Parapiptadenia blanchetii* (Benth.) Vaz & M.P. Lima	*Piptadenia blanchetii* Benth.	angico, guanambira	274,51,262
*		295	*Parapiptadenia zehntneri* (Harms) M.P. Lima & Lima	*Piptadenia zehntneri* Harms	angico, angico monjolo, faveira, guanabira, inhambira, fava	280,34,170,274,180 174,51,106,262,337
*	113	296	*Piptadenia moniliformis* Benth.		rama/angico-de-bezerro	280,17,397,262
*		297	*Piptadenia obliqua* (Pers.) Macbr.		quipembe, quipé, catanduva, angico de bezerro,carrasco	18,34,174,200,51, 106,173,337,36
		298	*Piptadenia stipulacea* (Benth.) Ducke	*Pityrocarpa stipulacea* (Benth.) Brenan	jurema branca, jurema-de-besta	153,174,262,337, 36
*		299	*Piptadenia viridiflora* (Kunth) Benth.	*P.biuncifera* Benth.; *Pityrocarpa v.* (Kth) Br.	jiquiri,jacurutú,jacarutú,soroca, surucucú, espinheiro (M.Gerais)	280,17,140,22,31, 62,32,153,51,262
*	114	300	*Pithecellobium diversifolium* Benth.		carcarazeiro, espinheiro, brinco de saguim, orelha-de-macaco	280,17,18,153,51, 173,262,36
	115	301	*Stryphnodendron coriaceum* Benth.			293
		302	*Stryphnodendron piptadenioides* Marts.		angico-bravo	397,293
			PAPILIONOIDEAE			

	116	303	*Acosmium dasycarpum* (Vog.) Yakovl. **subsp.** *glabratum* (Benth.) Yakovl.	*Sweetia elegans* (Vog.) Benth; *S.dasycarpa* (Vog.) Benth.		51?,262
		304	*Acosmium fallax* (Taub.) Yakovl.	*Sweetia fallax* Taub.	lombo preto	262
	117	305	*Aeschynomene filosa* Mart. ex Benth.			17,262
		306	*Aeschynomene martii* Benth.	*A. arbuscula* Rizz.; *A. rizzinii* Schoen.&Ferr.	pau-de-fuso	397,262
*	118	307	*Amburana cearensis* (Fr. All.) A.C.Smith	*Torresea cearensis* Fr. Allem.	imburana de cheiro, cumarú, c. de cheiro, c.-da-caatinga, amburana, umburana,u. macho	280,17,18,22,33, 168,170,153,180, 106,173,262,337, 36
*	119	308	*Bocoa mollis* (Benth.) Cowan	*Swartzia mollis* Benth. *S. cearensis* Ducke	brinquinho, chocalhinho	17,18,200,262
	120	309	*Calopogonium velutinum* (Benth.) Amsh.	*Stenolobium velutinum* Benth.	caatinga-de-macaco, cipó-de-macaco	107,337?
	121	310	*Canavalia brasiliensis* Mart. ex Benth.			262
		311	*Canavalia dictyota* Piper	*C. amazonica* Piper		262
	122	312	*Coursetia rostrata* Benth.		cavany, caoang	262,253
		313	*Coursetia vicioides* (Nees&Mart.) Benth.			262,253
*	123	314	*Cratylia mollis* Mart. ex Benth.		camaratuba, camaratu	280,17,18,153,262
		315	*Cratylia nuda* Tul.			262
	124	316	*Dalbergia catingicola* Harms		jacarandá, coração-de-negro	51,262,105

*		317	*Dalbergia cearensis* Ducke		violeta, pau violeta, jacarandá violeta j.-cega-machado, violete	17,18,397,51,106, 36,105
		318	*Dalbergia decipularis* Rizz. & Matt.		sebastião-de-arruda	262,105
		319	*Dalbergia frutescens* (Vell.) Britt. **var.** *frutescens*	*D.variabilis* Vog.; *Pterocarpus frut.* Vell.	mata-pulga	397,337,105
		320	*Dalbergia glaucescens* (Mart.ex Benth.) Benth.	*Miscolobium glauc.* Mart. ex Benth.		262,105
		321	*Dalbergia miscolobium* Benth.	*D.violacea*(Vog.)Malm.	canela-de-burro	262,105
	125	322	*Dioclea glabra* Mart. ex Benth.	*D.leiophylla* Ducke		262
		323	*Dioclea grandiflora* Mart. ex Benth.		mucunã, mucunã de caroço	17,153,180,106, 262,337,36
		324	*Dioclea guianensis* Benth. **var.** *lasiophylla* (Benth.) Maxwell	*D. lasiophylla* Mart. ex Benth.		262
	126	325	*Discolobium hirtum* Benth.			174,262
*	127	326	*Erythrina velutina* Willd.	*E. aurantiaca* Ridley	mulungú, bico-de-papagaio	280,17,18,283,248, 153,51,106,173,262
*	128	327	*Geoffroea striata* (Willd.) Morong	*G.superba* Kunth; *G. spinosa* Jacq.?	marizeiro, umarí, mari, "árvore que chora" (Paraíba)	280,17,18,31,62, 34,51,262,36
*	129	328	*Lonchocarpus araripensis* Benth.	*Derris araripensis* ?	angelim	18,28,262
		329	*Lonchocarpus campestris* Benth.		ingá-de-porco	51,262,282
*		330	*Lonchocarpus sericeus* (Poir.) Kunth	*Derris sericea* (Kunth) Ducke ?	ingá, cabelouro da caatinga, ingazeira, angelim	17,415,28,208,51, 106,262,337

		331	*Lonchocarpus virgilioides* Benth.			262
	130	332	*Luetzelburgia andrade-limae* Lima		pau d'anta, banha-de-galinha	32,272,262
*		333	*Luetzelburgia auriculata* (Fr.All.) Ducke	*Tipuana auriculata* Fr. All.;*L. pterocarpoides* Harms	angelim da caatinga, pau-pedra, pau-mocó	28,397,33,271,51, 262,337
		334	*Luetzelburgia bahiensis* Yakovl.		moela-de-galinha, sipipira	397,51,262
	131	335	*Machaerium acutifolium* Vog.		(se)bastião-de-arruda	208,262
		336	*Machaerium angustifolium* Vog.		sete-capotes, espinheiro, piquiá-pedra	29,262
		337	*Machaerium leucopterum* Vog.			262
		338	*Machaerium punctatum* (Poir.) Pers.	*M.villosulum* Mart.	jacarandá	262
	132	339	*Myroxylon balsamum* (L.) Harms	*M.peruiferum* L.f. [Stirton (*in sched.*)]	bálsamo	17,18,415,62, h.s.
	133	340	*Platymiscium obtusifolium* Harms		cedro bravo	280,262
		341	*Platymiscium zehntneri* Harms	[*P.floribundum* Vogel]	putumniú, jacarandá-canudo	280,51,262
	134	342	*Platypodium elegans* Vog.		chorão, jacarandá branco, alecrim, pitanguinha	29?,153,174,51, 262
	135	343	*Poecilanthe falcata* (Vell.) Heringer		chorão, carrancudo	17,18,28,51
		344	*Poecilanthe subcordata* Benth.			262
*		345	*Poecilanthe ulei* (Harms) Arr. & Rudd	*Machaerium ulei* Har.	besouro, carrancudo, mucitaíba	51,262
	136	346	*Pterocarpus ternatus* Rizzini		pau-sangue	395,397,262

		347	*Pterocarpus villosus* (Mart. ex Benth.)Benth.	*Amphymenium villosum* Mart.ex Bent.		262
		348	*Pterocarpus violaceus* Vog. **var.** *angustifolia* Benth.		pau-sangue	51,262
		349	*Pterocarpus zehntneri* Harms		pau-sangue	262
	137	350	*Riedeliella graciliflora* Harms	*R.hassleri* (Chod.) Harms; *Sweetiopsis hassleri* Chodat	cipó?	32,262
		351	*Riedeliella magalhaesii* (Rizz.)L.& Vaz	*Itaobimia mag.* Rizz.	levanta-foice	273
	138	352	*Sesbania exasperata* Kunth		canafístula-de-lagoa, manjerioba	17,174,262
	139	353	*Swartzia apetala* Raddi **var.** *apetala*	*Tounatea apetala* (Rad.)Taub.	coração-de-negro, fruto de urubú	127
*	140	354	*Zollernia ilicifolia* (Brongn.) Vog.	*Z. securidacifolia* Benth.	pau-santo, mocutaíba, pau-ferro, laranjeira brava, corazeiro	18,51,262
23			FLACOURTIACEAE			
	141	355	*Prockia crucis* P.Browne ex L. *s. lato*	*P.bahiensis* Turcz.		427,208
24			KRAMERIACEAE			
	142	356	*Krameria tomentosa* St.-Hil.			208,200,425
25			MALPIGHIACEAE			
	143	357	*Dicella bracteosa* (Adr.Juss.) Griseb.			329,208
	144	358	*Galphimia brasiliensis* (L.) Adr.Juss.			280,329,208
	145	359	*Heteropterys syringifolia* Griseb.			329,208

		360	*Heteropterys trichanthera* Adr.Juss.			329,208
	146	361	*Ptilochaeta bahiensis* Turcz.		estralador	329,397
	147	362	*Stigma phyllon auriculatum* (Cav.) A.Juss.			329,208,170
26			MALVACEAE			
	148	363	*Gaya aurea* St.-Hil.		malva	34,36
*		364	*Gaya gaudichaudiana* St.-Hil.			208,34
	149	365	*Herissantia crispa* (L.) Briz.		malva branca, m.-de-lavar-prato	34,400,106
*		366	*Herissantia tiubae* (K.Schum.) Briz.	*Bogenhardia tiubae* (Sch.) H. Mont.	mela-bode, melosa, malva-visguenta	332,168,208,34,153 106,337?,36,282
	150	367	*Pavonia andrade-lima* H.Mont.		tampa-cabaça	400,200
		368	*Pavonia humifussa* Juss.			200
		369	*Pavonia martii* Mart. ex Colla			208,282
*	151	370	*Sida cordifolia* L.		malva de veludo, malva-benta, malva-babenta, malva branca	17,34,153,106, 337,36
		371	*Sida galheirensis* Ulbr.		malva alta, malva-folha-miúda, malva grossa, malva branca	208,34,153,400, 174,106,212
		372	*Sida micrantha* St.-Hil.		malva alta, malva-capa-garote	208,153,106
	152	373	*Wissadula contracta* (Link) R.E. Fries			208
		374	*Wissadula patens* (St.-Hil.) Gürke			208
27			MELIACEAE			
	153	375	*Trichilia hirta* L.		cedro-canjerana, jitó or gitó (?)	208,350,153?,51

28			MORACEAE			
	154	376	*Brosimum gaudichaudii* Tréc.		inharé, embaré, minaré	397,153,51,337?
·	155	377	*Maclura tinctoria* (L.) Don ex Steudel	*Chlorophora t.* (L.)Bth.	amora, amoreira	397,51
29			MYRTACEAE			
	156	378	*Campomanesia eugenioides* (Cam.)Leg. **var.** *desertorum* (DC.) Landrum	*C.dardanolimai* Matt. & Legr.;*Psidium d.*DC.		252
30			NYCTAGINACEAE			
	157	379	*Bougainvillea glabra* Choisy			280,29?,208
	158	380	*Pisonia tomentosa* Casaretto		joão-mole, pau-piranha, maria-mole	22,153?,51,106, 173
31			OLACACEAE			
	159	381	*Schoepfia brasiliensis* DC.	*S.obliquifolia* Turcz.; *S. elliptica* All. ex Glaz.		208,428
*	160	382	*Ximenia americana* L.	*X.inermis* L.; *Amyris arborescens* P.Browne	ameixa	140,22,428,51, 173, 337
		383	*Ximenia coriacea* Engler			208,428
32			PHYTOLACCACEAE			
	161	384	*Gallesia integrifolia* (Spreng.) Harms	*G.gorazema* (Vell.) Moq.	pau d'alho, muirarema	403,51,360
	162	385	*Petiveria alliacea* L.		tipi	478,153
	163	386	*Phytolacca dioica* L.			35,51, h.s.

	164	387	*Seguieria aculeata* Jacq.	*S.parvifolia* Benth.; *S.guaranitica* Speg.		403
33			POLYGONACEAE			
	165	388	*Ruprechtia laxiflora* Meissn.	*R.polystachya* Gris.; *R. glauca* Meissn.	caixão	120,62,208,36, h.s.
*	166	389	*Triplaris gardneriana* Wedd.	*T. pachau* Mart.	pajeú, pajaú	17,140,18,415,31, 32,153,51
34			RHAMNACEAE			
	167	390	*Alvimiantha tricamerata* Grey-Wilson			208
	168	391	*Ziziphus cotinifolia* Reiss.			208,51, h.s.
*		392	*Ziziphus joazeiro* Mart.		juazeiro, juá, joa, joá-babão	280,17,18,168,34, 170,153,180,51,106 173,337,36,282
35			RUBIACEAE			
	169	393	*Alseis floribunda* Schott		goiabeira brava	208,435,51, h.s.
		394	*Alseis involuta* Schum.			h.s.
	170	395	*Coccocypselum dichroolasium* Mart.			208
	171	396	*Coutarea hexandra* (Jacq.) K. Schum.		quina-quina	208,153,435,51
	172	397	*Guettarda angelica* Mart. ex Müll.Arg.		açoita cavalo, angelica	397,32,208
	173	398	*Machaonia spinosa* Cham. & Schlecht.			280,51
	174	399	*Randia armata* (Sw.) DC.	*R.spinosa*(J.)Karst.;*Bas anacantha s.* (J.)Sch.	quatro-espinhos, limão-bravo	280,439,208,153?, 435

	175	400	*Simira* sp. Aublet	*Sickingia* sp. Willd.	pereiro-vermelho, pereiro da tinta, candeia-braba	439,32,153,435, 180,51,106, h.s.
36			RUTACEAE			
	176	401	*Balfourodendron riedelianum* (Engler) Engler		mucambo, pau-chumbo	208,400,51
37			SAPINDACEAE			
	177	402	*Sapindus saponaria* L.		sabão-de-soldado, sabonete	138,397,180,51
	178	403	*Serjania comata* Radlk.		ariú, saia-de-ariú	36,282
		404	*Serjania glabrata* Kunth		saia-de-cunhâ	375,208
38			SAPOTACEAE			
	179	405	*Micropholis gnaphaloclados* (Mart.) Pierre	*Lucuma gnaphaloclados* Mart.		351
	180	406	*Pouteria gardneriana* (DC.) Radlk.	*Lucuma gard.* DC.		153,351
*	181	407	*Sideroxylon obtusifolium* (Roem. & Schult.) Pennington **subsp.** *obtusifolium*	*Bumelia obtusifolia* Roem. &Schul.; *B. sartorum* Mart.; *B. fragrans* Ridley	quixabeira, quixabá preta, rompe-gibão	17,22,168,170,435, 51,106,173,36, 351
39			SOLANACEAE			
	182	408	*Brunfelsia clandestina* Plowman			358
		409	*Brunfelsia uniflora* (Pohl) D.Don	*Franciscea unifl.* Pohl	manacá	140,357,208, h.s.
	183	410	*Solanum chaetacanthum* Dunal		budim	208,106

		411	*Solanum granuloso-leprosum* Dunal	*S. riparium* Pers.; *S. verbascifolium* L.		208, h.s.
40			STERCULIACEAE			
	184	412	*Ayenia blanchetiana* K.Schum.			128
		413	*Ayenia erecta* Mart. ex Schum.		cabacinha	128,106,409
		414	*Ayenia hirta* St.-Hil. & Naud.			128
		415	*Ayenia tomentosa* L.			128,208
	185	416	*Byttneria scabra* L.	*B.salicifolia* Humb. & Bonpl. ex Schultes		280,208
	186	417	*Helicteres eichleri* K.Schum.		saca-rolha	280,400,106
		418	*Helicteres mollis* K.Schum.		saca-rolha, guaxumba, cachimbeira	138,400,200?
		419	*Helicteres velutina* K.Schum.			208,400
	187	420	*Melochia betonicifolia* St.-Hil.	*M.cordiformis* St.-Hil.; *M.nepetoides* St.-Hil.		196
		421	*Melochia tomentosa* L. **var.***tomentosa*			196,208,34,153, 200
	188	422	*Sterculia striata* St.-Hil. & Naud.		chichá, xixá, castanheta	138,12,31,32, 444
*	189	423	*Waltheria ferruginea* St.-Hil.			34,153,200
41			TILIACEAE			
	190	424	*Luehea candicans* Mart. & Zucc. **var.** *candicans*	*L.villosa* Mart.& Zucc.; *L. uniflora* St.-Hil.; *L.microphylla* Pohl	açoita-cavalo, malvão-bravo	397,208,130,51

42			ULMACEAE			
	191	425	*Celtis pubescens* (Kunth) Sprengel	*C.boliviensis* Pl.ex DC; *C. brasiliensis* Gard. ex Planchon		44, h.s.
	192	426	*Phyllostylon brasiliensis* Capanema		carne-d'anta, pau-branco, vareteiro	103,35,400,51
43			VELLOZIACEAE			
	193	427	*Xerophyta cinerascens* Roem. & Schult.	*Vellozia ciner.* Mart.	canela-de-ema, perna-d'ema	207,153,36
		428	*Xerophyta plicata* (Mart.) Spreng.	*Vellozia plicata* Mart.	canela-de-ema	280,32,36(p.12)
44			VERBENACEAE			
	194	429	*Amasonia campestris* (Aubl.) Mold.			208,153?
	195	430	*Lantana caatingensis* Moldenke			208
		431	*Lantana camara* L.		cambará, camara	280,32,153,400, 106,173,337,282
	196	432	*Lippia bahiensis* Moldenke			208
		433	*Lippia gracilis* Schauer			280,208,400
	197	434	*Stachytarpheta sanguinea* Mart.ex Sch.			280,208
*	198	435	*Vitex gardneriana* Schauer		salgueiro, jaramataia, jerematai a	138,17,18,415, 397,51,337,36
45			VITACEAE			
	199	436	*Cissus coccinea* Mart. ex Planch.		cipó-gordo, cipó-de-cobra	32,106,36
		437	*Cissus simsiana* Roem. & Schult.		cipó-de-vaqueiro, parreira	32,208,106

4.3- Woody and succulent species of the Subandean Piedmont Forests:

In the floristic list of the woody and succulent species of the Subandean Piedmont Forests, those indicated with an asterisk (*) correspond to taxa known to occur only in the Bolivian sector of this vegetation unit, and whose presence in the southern Argentine sector is yet to be proved. The taxa indicated with a capital letter (C) are regarded as Chaco intruders into the Subandean Piedmont Forests, generally coming from the adjoining Sierra Chaco. In the 'Main Synonym' column the names between brackets ([...]) are common identification mistakes or binomials wrongly applied to the entities shown in the 'Species Name' column, not to be treated as taxonomic synonyms. In the 'References' column, h.s. stands for 'herbarium specimens' in those cases in which exsiccata have been taken by the present author as evidence of the alleged presence of the species in the area.

Fly Nº	Gen Nº	Sp Nº	SPECIES NAME	MAIN SYNONYM	VERNACULAR NAME	REFERENCES
1			ACHATOCARPACEAE			
	1	1	*Achatocarpus praecox* Gris.	*A. nigricans* Triana	palo de tinta, palo mataco, ruma caspi, tala negro	9,77
2			AMARANTHACEAE			
	2	2	*Chamissoa altissima* (Jacq.) Kunth			97
3			ANACARDIACEAE			
	3	3	*Astronium urundeuva* (Fr.All.) Engler		urundel, cuchi	48,97
	4	4	*Loxopterigium grisebachii* Hieron. & Lorentz ex Griseb.		urundel amarillo	46,379

*	5	5	*Schinopsis brasiliensis* Engler **var.** *brasiliensis*		quebracho, cuchi, soto	217,304
*			**var.** *glabra* Engler	*S.glabra* (En.)B.&Mey.		217,304
C		6	*Schinopsis haenkeana* Engler	*S. marginata* Engler; *S. lorentzii* **var.** *marginata* (Eng.)Cabr.	horco quebracho, q. colorado del cerro, q. serrano	136,379
	6	7	*Schinus gracilipes* Johnston **var.** *gracilipes*		molle de la quebrada, molle del cerro, horco-molle	134,45
			var. *pilosus* Barkley			45
		8	*Schinus piliferus* I.M.Johnston **var.** *piliferus*		molle, m.blanco, m. de Tucumán	45
			var. *cabrerae* (Barkl.)Barkley		molle, m.blanco, m.colorado	45
		9	*Schinus venturii* Barkley			45
4			ANNONACEAE			
	7	10	*Rollinia occidentalis* R.E. Fries		chirimoya, chirimoya del monte	256
5			APOCYNACEAE			
*	8	11	*Aspidosperma parvifolium* A.DC.		palo amarillo	286
	9	12	*Rauvolfia schuelii* Speg.		lecherón negro, leche-leche	256
6			ARALIACEAE			
	10	13	*Pentapanax angelicifolius* Griseb.		sacha-paraíso, pino, albiche	134,302,136,77
7			ARECACEAE			
	11	14	*Acrocomia chunta* Covas & Ragonese		chonto, chunta	302,97,355

C	12	15	*Copernicia alba* Morong	*C. australis* Becc.	carandá, caranday	183,132
	13	16	*Trithrinax schizophylla* Drude		palma, saro, saho	379,354
8			ASCLEPIADACEAE			
	14	17	*Marsdenia altissima* (Jacq.) Dugand	*M.mollissima* Fourn.		302,317
	15	18	*Schubertia schreiteri* Desc. & Meyer			134,302,97
9			ASTERACEAE			
	16	19	*Barnadesia odorata* Griseb.		trampa de gato, clavel	134
	17	20	*Chaenocephalus heterophyllus* Griseb.			210,134
	18	21	*Cnicothamnus lorentzii* Griseb.	=*C.azafran* ? [379]	azafrán, cejranilla, dominguillo	134,136,97
	19	22	*Dasyphyllum brasiliense* (Spreng.) Cabrera	*Flotovia brasiliensis* (Sp.)Cabr.;*Chuquiraga glabra* (Spr.)Baker; *Ch. brasiliensis* (Spr.)OK.		93,94
	20	23	*Eupatorium lasiophthalmum* Griseb.	*E. hiemale* Lillo	malvón	134,256
		24	*Eupatorium saltense* Hieron.			256
	21	25	*Lagascea mollis* Cav.			440
	22	26	*Pseudogynoxys benthamii* (Gris.) Cabr.			97
	23	27	*Senecio deferrens* Griseb.			210
		28	*Senecio peregrinus* Griseb.			303
	24	29	*Tessaria integrifolia* Ruiz & Pavón		palo bobo, aliso, a.del río, bobo,etc	9,256
	25	30	*Vernonia cincta* Griseb.			183
		31	*Vernonia fulta* Griseb.	=*V.squamulosa* ?	Santa Rosa	303,379?,97

10			BIGNONIACEAE			
	26	32	*Amphilophium sandwithii* Fabris			164
		33	*Amphilophium vauthieri* DC.	*A.paraguariense* Hassl. ex Schulz		164
	27	34	*Arrabidea corallina* (Jacq.) Sandwith	*Bignonia cor.* Jacq.; *A. rhodantha* Bur.& Sch.		164
		35	*Arrabidea selloi* (Spreng.) Sandwith	*Bignonia selloi* Spreng.		164
	28	36	*Clytostoma callistegioides* (Cham.) Bur. ex Griseb.	*Bignonia call.* Cham.; *B.speciosa* Tw.ex Hook.	alegría de la mañana, dama del monte	164,191
	29	37	*Jacaranda cuspidifolia* Mart. ex DC.	*J.chelonia* Gris.[Symb]		164,306
		38	*Jacaranda mimosifolia* D.Don	*J.chelonia* Gris.[Pl.L.]; *J.ovalifolia* R.Br.	jacarandá, tarco	303,164,136,306
	30	39	*Macfadyena unguis-cati* (L.) Gentry	*Doxantha uc.*(L.)Miers		164,97
	31	40	*Melloa populifolia* (DC.) Britton	*Bignonia populifolia*DC		164
	32	41	*Paradolichandra chodatii* Hassler			164
*	33	42	*Tabebuia aurea* (Manso) ? [Gentry, *in litt.*]	*T.caraiba* (Mart.) Bur.	paratodo	h.s.
		43	*Tabebuia impetiginosa* (Mart. ex DC.) Standley	*T.avellanedae* Lorentz ex Griseb.;*T.ipe* (Mart. ex Schum.) Standley	lapacho, lapacho rosado	303,164,97

		44	*Tabebuia ochracea* Cham. **subsp.** *heteropoda* (DC.) A. Gentry[1]	*T.lapacho* (Schum.) Sandw.	lapacho amarillo, lapacho amarillo salteño	164,256,190, h.s.
	34	45	*Tecoma garrocha* Hieron.		guaranguay colorado, guarán colorado,nosto, garrocha	134,164,379
		46	*Tecoma stans* (L.) Juss. ex Kunth		guaranguay amarillo, guarán amarillo	134,303,164,136, 379
		47	*Tecoma tenuiflora* (DC.) Fabris	*Bignonia tenuiflora* DC	guaranguay del cerro	164
11			BOMBACACEAE			
	35	48	*Ceiba chodatii* (Hassler) Gibbs & Semir comb. ined.	*Chorisia insignis* Kunth	palo borracho, yuchán, painero, algodonero, etc.	303,136,9,97, 77, Gibbs (p.comm.)
	36	49	*Eriotheca roseorum* (Cuatrecasas) A. Robyns	*Bombax roseorum* Cuat.;*Tartagalia rubra* Capurro; *T. roseorum* (Cuatr.)Meyer		102,399
	37	50	*Pseudobombax argentinum* (Fries) Robyns	*Bombax argentinum* Fries; *B.marginatum* (St.-Hil.,Juss.& Camb.) K. Schum.	soroche	134,399,97,256
12			BORAGINACEAE			
	38	51	*Cordia alliodora* (Ruiz & Pavon) Oken			210,193

[1] Specimens of *T. lapacho* at K have been identified by Gentry as *T. ochracea* subsp. *heteropoda* , whereas in Gentry (1982) he states they are subsp.*ochracea*.

		52	*Cordia trichotoma* (Vell.) Arrab. ex Steud.	[complex with *C. alliodora* (R.&P.) Oken]	afata, afata blanca, afata grande	9,97,256,193
	39	53	*Patagonula americana* L.		guayaibí, g.blanco, sauquillo, guayabil	134,97,256
	40	54	*Saccelium lanceolatum* Humb.& Bonpl.		guayabil, g.negro, guayibil	134,302,256
	41	55	*Tournefortia lilloi* Johnst.			134
		56	*Tournefortia rubicunda* Salzm. ex DC.			134
13			BROMELIACEAE			
	42	57	*Aechmea distichantha* Lemaire		caraguatá	379,432
C	43	58	*Bromelia serra* Grisebach		chaguar, cardo gancho	9
C	44	59	*Dyckia ferox* Mez		chaguar	432
C		60	*Dyckia floribunda* Grisebach	*D. chaguar* Castell.	chaguar	432
		61	*Dyckia velascana* Mez			432
14			BUDDLEJACEAE			
	45	62	*Buddleja albotomentosa* R.E. Fries			97
15			CACTACEAE			
	46	63	*Brasiliopuntia brasiliensis* (Willd.) Berger	*Opuntia argentina* Gr.; *O.hieronymi* Gris.		76,112,90
C	47	64	*Cereus validus* Haworth	*C.forbesii* Otto	ucle	9
C	48	65	*Cleistocactus smaragdiflorus* (Web.)Br.& Rose	*Cereus smaragdiflorus* Weber	uvillinche, cogote de suri	240

*	49	66	*Espostoa guentheri* (Kupp.) Buxbaum	*Vatricania guentheri* (Kupp.) Backeberg		89,90,42
C	50	67	*Opuntia discolor* Britton & Rose			76,9
C		68	*Opuntia kiskaloro* Spegazzini		quiscaloro	9
	51	69	*Pereskia sacharosa* Grisebach	*P. moorei* Br.& Rose	sacha-rosa, cuguchi, guyapa	90,9,260
	52	70	*Quiabentia pflanzii* (Vaupel)Berger	*Q. chacoensis* Back.; *Pereskia pflanzii* Vaup	sacha-rosa, amendacaru, achuma, tunilla	108
*		71	*Quiabentia verticillata* (Vaupel)Berger		amendacaru-rai, achuma, oreja de perro	108
*		72	*Quiabentia zehntneri* (Br.& R.)Br.&Rose	*Pereskia z.* Br. & Rose		108
	53	73	*Trichocereus terscheckii* (Parm.)Br.&R.	*Cereus terscheckii* Pm.	cardón grande	239
		74	*Trichocereus thelegonoides* (Speg.) Britton & Rose	*Cereus thelegonoides* Speg.		239
		75	*Trichocereus thelegonus* (Web.)Br.&R.	*Cereus thelegonus* Web	cola de león	239
16			CAPPARIDACEAE			
C	54	76	*Capparis retusa* Grisebach var.*retusa*	*C. cynophallophora* L. **var.** *retusa* (Gris.)OK	sacha-poroto	9
		77	*Capparis tweediana* Eichler		sacha membrillo, s.coca, yerba de la comadreja, cayampa	302
17			CARICACEAE			
	55	78	*Carica glandulosa* Pavón ex A.DC.	*C. gossypiifolia* Gris.	higuera/mamón del monte	134,43

		79	*Carica quercifolia* (St.-Hil.) Hieron.	*C.l anceolata* (A.DC.) Hier.;*Vasconcellea quercifolia* St.-Hil.	sacha-higuera, higuera/mamón del monte, higuerón, papaya silvestre	134,303,379,43, h.s.
	56	80	*Jacaratia corumbensis* Kuntze	*J. hassleriana* Chod.	yacón, Akol-yacón, cipoy	302,43
18			CELASTRACEAE			
	57	81	*Maytenus cuezzoi* Legneme			256
C		82	*Maytenus viscifolia* Grisebach		tapia, palta, asperillo, chasqui yuyo, mucamo	136
	58	83	*Plenckia integerrima* Lundell	*Viposia integerrima* (Lundell) Lundell	palo blanco	134,136,379
19			COCHLOSPERMACEAE			
	59	84	*Cochlospermum tetraporum* Hallier	*C.zahlbruckneri* Ost.; *C.argentinensis* (Speg.) Haum.	queñoa, palo papel, árbol de papel	134,379,9,364, 256
*		85	*Cochlospermum vitifolium* (Willd.) Spreng.	[*C.regium* (Schr.)Pilg.; *C.insigne* St.-Hil.]		364
20			COMBRETACEAE			
*	60	86	*Combretum guanaiense* Rusby			163
*		87	*Combretum leprosum* Martius		mapaiso	163
	61	88	*Terminalia triflora* (Griseb.) Lillo	*T.balansae* (OK.)K.Sch. *T.hassleriana* Chod.	lanza amarila, lanza, amarillo de río	162,134,303,136, 410,97
21			CONVOLVULACEAE			

	62	89	*Ipomoea carnea* Jacq. **subsp.** *fistulosa* (Mart. ex Choisy) D. Austin	*I. fistulosa* Mart. ex Choisy	floripón	333
		90	*Ipomoea crinicalyx* Moore			333
C		91	*Ipomoea hieronymi* (OK.) O'Donell			333
22			ELAEOCARPACEAE			
	63	92	*Mutingia calabura* L.		sacha guinda	134,97,256
23			ERYTHROXYLACEAE			
	64	93	*Erythroxylum argentinum* O.E. Schulz		ajicillo, sacha ají, coca del monte	418,136
		94	*Erythroxylum cuneifolium*(Mar.)Schulz		coca del monte	418,256
24			EUPHORBIACEAE			
	65	95	*Cnidoscolus vitifolius* Mill. ex Pohl **var.** *cnicodendron* (Griseb.) Pax	*C.cnicodendron* Griseb.	ortiguilla, ortiga, cerraja árbol, piñón de ortiga	134,9,256
	66	96	*Croton beetlei* Croiz.			256
		97	*Croton densiflorus* Pax & Hoffmann		sacha-chirimoya, sangre de drago	134,256
	67	98	*Ditaxis breviramea* (Müll. Arg.) Pax & Hoffm.	*Argythamnia breviramea* Müll.Arg.		335
	68	99	*Euphorbia oranensis* (Croizat) Subils			i42
C	69	100	*Jatropha hieronymi* O.Ktze		piñón, sacha higuera	134,346,256
	70	101	*Manihot anomala* Pohl emend. Rogers & Appan **subsp.** *pavoniana* (Müll.Arg.) Rogers & Appan	*M. heterophylla* Pohl; *M. pavoniana* Müll.Arg.		402
		102	*Manihot grahami* Hooker	*M.tweediana* M.Arg.	mandioca brava	402

		103	*Manihot guaranitica* Chodat & Hassler **subsp.** *guaranitica*	*M. fiebrigii* Pax & Hoffm.; *M. recognita* Pax		402
	71	104	*Parodiodendron marginivillosum* (Speg.) A.T. Hunziker	*Phyllanthus marginivillosa* Spegaz.	lenteja	256
	72	105	*Phyllanthus acuminatus* Vahl		chirrincha	256
	73	106	*Sapium saltense* (O'Don.&Lour.) Jablonski	*S.haematospermum*M. Arg.**var.***saltensis* O&L.	lecherón, curupí	302,136,233
	74	107	*Sebastiania brasiliensis* Spreng.		leche-leche, palo de leche	136,379
		108	*Sebastiania klotzschiana* (M.A.)M.Arg.		blanquillo, amarillo	134,379
25			FABACEAE			
			CAESALPINIOIDEAE			
	75	109	*Bauhinia argentinensis* Burkart **var.** *megasiphon* (Burk.) Fortunato	*B. megasiphon* Burkart		178
		110	*Bauhinia forficata* Link **subsp.** *pruinosa* (Vog.) Fort. & Wund.	*B. candicans* Benth.; *B. pruinosa* Vog.	pata de vaca, pata de buey, caoba, falsa caoba	136,178
		111	*Bauhinia mollis* (Bong.) D. Dietrich **var.** *notophila* (Gris.) Fortunato	*B. notophila* Gris.	pata de vaca, uña de tigre	177,178
	76	112	*Caesalpinia floribunda* Tul.		morochillo, momoqui	84,256
C		113	*Caesalpinia paraguariensis* (D.Parodi) Burkart	*C. melanocarpa* Gris.	guayacán, guayacán negro	302,84

	77	114	*Chamaecrista calycioides* (Coll.)Greene **var.** *calycioides*			232
*	78	115	*Copaifera paupera* (Herzog) Dwyer	*Copaiba paupera* Herz. *C.langsdorffii* Desf. **var.** *peruviana* Mcbr.	copaiba blanca	144
	79	116	*Gleditsia amorphoides* (Gris.) Taub.	*Garugandra amorphoides* Gris.	coronillo, espina corona, caranchí, carandí	84,97,256
*	80	117	*Peltophorum dubium* (Spreng.) Taub.	*Caesalpinia dubia* Spr. *P. vogelianum* Benth.		h.s.
	81	118	*Pterogyne nitens* Tul.		tipa, tipa colorada, palo mortero, palo coca	302,84,9,97
	82	119	*Senna pendula* (Willd.) Irwin & Barneby	*Cassia bicapsularis* L. **var.** *eriocarpa* Gris.	yerba de burro, sen, muveva, pitó-movéva	134,84,97,232
		120	*Senna spectabilis* (DC.) Ir. & Barneby **var.** *spectabilis*	*Cassia spectabilis* DC.; *C.carnaval* Spegazzini	carnaval, palo flojo	84,9,97,256, 232
			MIMOSOIDEAE			
	83	121	*Acacia albicorticata* Burkart		tusca blanca, aromo, tataré, espinillo blanco, espino blanco	84,97,256,117
		122	*Acacia etilis* Spegazzini		garabato guiador, g.de 4 caras, g. blanco, guayacán	379,117
		123	*Acacia parviceps* (Speg.) Burkart	*A.adhaerens* (Mart.) Bth. **var.***parviceps* Sp.	garabato blanco, yapán	379,117

		124	*Acacia tucumanensis* Grisebach	*A. riparia* auct.	garabato, g. negro, g. blanco	84,9,117
	84	125	*Albizia polyantha* (Spreng.f.) Lewis	*Cathormion polyanthum* (Spr.)Bk.; *Pithecellobium multiflorum*(Kth)Benth	palo flojo, timbó, timbó blanco, pacará blanco, tarco, sacha-monte	134,9
	85	126	*Anadenanthera colubrina* (Vell.) Bren. **var.** *cebil* (Griseb.) Altschul	*Piptadenia macrocarpa* Benth.; *P.m.* **var.** *cebil* (Gris.)Ch.&Hassl.; *A. macrocarpa*(Bent.)Br.	cebil, cebil moro, cebil colorado	134,302,84,303, 11,9,97
	86	127	*Calliandra formosa* (Kunth) Benth.			302,84
	87	128	*Desmanthus virgatus* Willd.	*Mimosa virgata* L.		84
	88	129	*Enterolobium contortisiliquum* (Vell.) Morong	*E. timbouva* Mart.; *Mimosa cont.* Vellozo	pacará, timbó colorado, oreja de negro	84,303,136,97, 77
	89	130	*Inga saltensis* Burkart		pacay, inga	84,256
	90	131	*Mimosa polycarpa* Kunth			84
		132	*Mimosa sensibilis* Grisebach			84
		133	*Mimosa stenoptera* Benth.			84
		134	*Mimosa velloziana* Mart.			84
	91	135	*Parapiptadenia excelsa* (Gris.) Burkart	*Piptadenia ex.* (Gris.) Lil.; *P.communis* Bth. **var.** *excelsa* Gris.	horco cebil, cebil blanco, sacha-cebil	134,136,97,77

	92	136	*Piptadenia viridiflora* (Kunth) Benth.	*P.biuncifera* Benth.; *Pityrocarpa v.* (Kth) Br.	vilcarán, tjarca, garabato, carancho, guaranchillo	84,379,256
	93	137	*Pithecellobium chacöense* Burkart		palo overo, palo barroso	84,379,220,256
		138	*Pithecellobium grisebachianum* Harms	*Calliandra grisebachiana* Speg.	palo barroso, guayacán, guayacán blanco	84,220,256
		139	*Pithecellobium scalare* Grisebach	*P.tortum* Mart. f. *scalare* (Gris.) Hassler	palo cascarudo, espinillo, tatané	84,97,220
C	94	140	*Prosopis nigra* (Grisebach)Hieronymus **var.** *nigra*	*P. dulcis* Kunth var. *australis* Bentham	algarrobo negro, árbol negro	9
			PAPILIONOIDEAE			
	95	141	*Aeschynomene rudis* Benth.			84
	96	142	*Amburana cearensis* (Fr. All.) A.C.Smith	*Torresea cearensis* Fr. Allem.	roble del país, roble, cedro salteño, palo trébol, roble salteño	303,84,9,97
	97	143	*Canavalia brasiliensis* Mart. ex Benth.	*C.gladiata* Lor.& Gris.		84
	98	144	*Cascaronia astragalina* Grisebach		cascarón, tipa amarilla	84,136,256
	99	145	*Coursetia brachyrhachis* Harms	*Tephrosia craccoides* Lillo		84,253
		146	*Coursetia hassleri* Chodat [2]	*C. guaranitica* Chod.; *Cracca corumbae* Hoeh		84,9,253, Lavin, *in litt.*
		147	*Coursetia hypoleuca* (Spegazzini) Lavin	*Poissonia hy.* (Sp.) Lil.; *Chiovendaea hy.* Speg.		84,253

[2] See footnote 4 in Section 4.1.

	100	148	*Erythrina dominguezii* Hassler	*E. chacöensis* Speg.	ceiba, ceibo, c.rosado, seibo chaqueño, seibo rosado	134,84,248,256
		149	*Erythrina falcata* Benth.	*E.crista-galli* L. **var.** *inermis* Speg.& Girola	ceiba, ceibo, seiba, seibo, s. de la selva,s.rosado,s.salteño, s.jujeño	134,84,136,379, 248
	101	150	*Geoffroea decorticans* (H.& Arn.) Burk. **var.** *subtropicalis* (Lillo) Burk.	*Gourleia dec.* Gill. **var.** *subtropicalis* Lillo	chañar, chañar arbóreo	83,84
*		151	*Geoffroea striata* (Willd.) Morong	*G.superba* Kunth; *G. spinosa* Jacq.?	almendrón (Peru)	83,84, h.s.
	102	152	*Lonchocarpus lilloi* (Hassler) Burkart	*L.nitidus* (Vog.)Benth. **var.** *lilloi* Hassler	sacha quina, quina blanca	84,97,256
*	103	153	*Machaerium acutifolium* Vog.			84, h.s.
	104	154	*Myroxylon balsamum* (L.) Harms	*M.peruiferum* L.f. [Stirton (*in sched.*)]	quina, kina, quina-quina, kina-kina, kina morada	134,84,9,97, 256,77
*	105	155	*Platypodium elegans* Vog.			h. s.
	106	156	*Psoralea higuerilla* Gill.	*P.higuera* Gris.	higuerilla	84
	107	157	*Sesbania exasperata* Kunth			84
*	108	158	*Swartzia jorori* Harms		jorori	127
	109	159	*Tipuana tipu* (Benth.) O.Kuntze	*Machaerium tipu* Benth.	tipa, tipa blanca, tipú, palo mortero	84,303,136,97, 77
26			FLACOURTIACEAE			
	110	160	*Casearia silvestris* Sw.		palo rajador, rajador, yerba de lagarto, quillero	256
	111	161	*Prockia crucis* P.Browne ex L. *s. lato*	*P.bahiensis* Turcz.		136,97

27			LAURACEAE			
	112	162	*Ocotea puberula* (Nees. & Mart.) Nees	*O.suaveolens* (Meissn.) Hassler ?	laurel, laurel del río, l. blanco, l. amarillo, l. mestizo, guaica	183,134
	113	163	*Phoebe porphyria* (Griseb.) Mez	*Nectandra por.* Gris.	laurel, l. de la falda, l. del cerro, l. tucumano, l. del monte	303,136
28			MALPIGHIACEAE			
*	114	164	*Galphimia brasiliensis* (L.) Adr.Juss.			329
	115	165	*Heteropterys syl vatica* Adr.Juss.			336
*		166	*Heteropterys syringifolia* Griseb.			329
		167	*Heteropterys umbellata* Adr.Juss.			336
	116	168	*Ptilochaeta nudipes* Grisebach		amarillo	336,329,256
*	117	169	*Stigma phyllon coloratum* Rusby			329
29			MALVACEAE			
	118	170	*Abutilon molle* ?			97
	119	171	*Pavonia eurychlamys* Ulbrich			247
		172	*Pavonia hirta* Sprengel	*P.glechomoides* St.-Hil.		247
		173	*Pavonia malvacea* (Vell.) Krap. & Crist.	*P. sepium* St.-Hil.		247
	120	174	*Sida cordifolia* L.			401
30			MELIACEAE			
	121	175	*Cedrela fissilis* Vellozo	*C.balansae* C.DC.; *C. macrocarpa* Ducke		430,350

		176	*Cedrela lilloi* C.DC.	*C. boliviana* Rusby; *C. steinbachii* Harms	cedro	183,430,136,350
		177	*Cedrela odorata* L.	*C.paraguariensis* Mart [*C.angustifolia* Sessé & Mociño ex C.DC.]	cedro, cedro salteño, cedro paraíso	97,256,350
	122	178	*Trichilia clausseni* C.DC.	*T.hieronymi* Gris.; *T. tartagalensis* C.DC.	dominguillo, mayan jtara, catiguá blanco, catiguá morotí	210,134,97,256, 350
31			MORACEAE			
	123	179	*Ficus maroma* Castellanos		maroma, gomero, aguaray	302,468,256,469
	124	180	*Maclura tinctoria* (L.) Don ex Steudel **subsp.** *mora* (Griseb.) Vázquez Ávila	*Chlorophora tinct.* (L.) Gaud.**subsp.***mora*(Gr.) Hassl.;*M.mora* Gris.	mora, mora colorada, mora amarilla, mora de la pampa	302,97,256,469
32			MYRSINACEAE			
	125	181	*Rapanea laetevirens* Mez		canelón, San Antonio	426,303,136
33			MYRTACEAE			
	126	182	*Eugenia uniflora* L.	*Stenocalyx micheli* (Lam.) Berg	arrayán	257,303,136,379
	127	183	*Myrcianthes cisplatensis* (Camb.) Berg	*Eugenia cisplatensis* Camb.	vil-vil, güili, sacha mato, arrayán, lapachillo, palo pelao	136,406
		184	*Myrcianthes mato* (Gris.) Mc Vaugh	*Acreugenia mato* (Gr.) Kaus.;*Eugenia m.* Gr.	mato, horco-mato, alpa-mato, sacha-mato	257,303,136,406, 77

		185	*Myrcianthes pungens* (Berg) Legrand	*Acreugenia p.* (Berg) Kaus.;*Eugenia p.* Berg	mato, guabiyú, arrayán negro, arrayán	257,134,9,406, 77
	128	186	*Siphoneugena occidentalis* Legrand		frutilla	256,371
34			NYCTAGINACEAE			
C	129	187	*Bougainvillea stipitata* Grisebach		alfiler, alfilerillo, tala falso, guáncar blanco, coronillo blanco	134,136
	130	188	*Pisonia zapallo* Grisebach	*P.ambigua* Heimerl	zapallo-caspi, mata pájaro, caspi zapallo	303,9,452,97, 256
	131	189	*Pisoniella arborescens* (Lag. & Rodr.) Standley **var.** *glabrata* Heimerl	*Pisonia hirtella* Kunth		210,134,452
35			OLACACEAE			
*	132	190	*Schoepfia tetramera* Herzog	*S.obliquifolia* Rusby		428
C	133	191	*Ximenia americana* L. **var.** *argentinensis* De Filipps	*X.americana* L. **var.** *oblonga* Gris.	pata, albaricoque, pata del monte	256,428
36			OPILIACEAE			
	134	192	*Agonandra excelsa* Grisebach		sacha pera, pata, meloncillo, sacha naranjo, caona	134,256
37			PHYTOLACCACEAE			
	135	193	*Hilleria latifolia* (Lam.) H.Walt.	*Mohlana latifolia* Moq.		302,9
	136	194	*Petiveria alliacea* L.		pipí	302,478,9,453
	137	195	*Phytolacca bogotensis* Kunth			303

	138	196	*Seguieria aculeata* Jacq.	*S.parvifolia* Benth.; *S.guaranitica* Speg.	verdenaza, espina del infierno	134,302,403
*		197	*Seguieria paraguayensis* Morong	*S. inermis* Walter		134,403
38			PIPERACEAE			
	139	198	*Piper aduncum* L. **var.** *cordulatum* (C.DC.) Yunquer	*P.angustifolium* R.& P. **var.***cordulatum* C.DC.		134,302,256
		199	*Piper medium* Jacq.			134,302
		200	*Piper tucumanum* C.DC.		no duro, lata de pobre, matico	134,136
39			POLYGONACEAE			
	140	201	*Coccoloba cordata* Chamisso		morilla, duraznillo morado, yana poco, mandor	134,302,136
		202	*Coccoloba tiliacea* Lindau		sacha pera, sacha mora	134,302,256,77
C	141	203	*Ruprechtia apetala* Weddell	*R. corylifolia* Gris.; *R. mollis* Wedd.; *R. boliviensis* Herzog	manzano del campo, duraznillo, d. colorado, sacha manzana, manzanillo	119,9,77
		204	*Ruprechtia laxiflora* Meissn.	*R.polystachya* Gris.; *R. glauca* Meissn.	virará, viraró, virará blanco	119,136,97
40			RHAMNACEAE			
	142	205	*Scutia buxifolia* Reissek	*Adolia bux.* (Reiss.)OK.	coronillo, coronillo colorado	155,234,97
C	143	206	*Ziziphus mistol* Grisebach		mistol, sacha mistol	9
		207	*Ziziphus oblongifolius* S. Moore			155
		208	*Ziziphus piurensis* Pilger			155

41			RUBIACEAE			
	144	209	*Calycophyllum multiflorum* Grisebach		palo blanco	210,183,302,93, 9,97,256
	145	210	*Coutarea hexandra* (Jacq.) K. Schum.		quina, cascarilla, dominguillo	134,302,256
	146	211	*Hoffmannia australis* Lillo			210,134,303
	147	212	*Manettia cordifolia* Martius			302
	148	213	*Pogonopus tubulosus* (DC.) K.Schum.		sacha-quina, virreina, flor del diablo, cascarilla, quina-quina	97,256
	149	214	*Randia armata* (Swartz) DC.	*R.spinosa*(J.)Karst.;*Bas anacantha s.* (J.)Sch.	sacha limón, sacha lima	303,136,64
42			RUTACEAE			
C	150	215	*Fagara coco* (Gill.) Engler	*Zanthoxylum coco* Gill.	coco, cocucho, sauco hediondo, cochucho	156,303,136,379, 97
		216	*Fagara naranjillo* (Griseb.) Engler	*Zanthoxylum n.* Gris.; *F.hieronymi* Engler	sacha limón, naranjillo, sacha-naranjo	156,136,9
		217	*Fagara nigrescens* Fries		sauquillo, sauco hediondo, naranjillo negro	156,256
		218	*Fagara pterota* L.	*Zanthoxylum p.* Kunth *F.pterota* (Kunth)Engl.	uña de tigre, uña de gato, teatín	156,256
		219	*Fagara rhoifolia* (Lam.) Engler	*Zanthoxylum rhoifolium* Lam.; *F. niederleinii* Engler		156,136,9

43			SANTALACEAE			
C	151	220	*Acanthosyris falcata* (Mart. & Eichl.) Grisebach		sacha pera, saucillo, sombra de toro hembra	136,9,150
44			SAPINDACEAE			
	152	221	*Allophyllus edulis* (St.-Hil.) Radlkofer	*Schmidelia edulis* St.-Hil.	chalchal, comida de paloma	136,9,97
	153	222	*Athyana weinmannifolia* (Gris.) Radlk.	*Thouinia wein.* Gris.	quebrachillo, q.colorado, tarco	134,302,9,256
	154	223	*Cupania vernalis* Cambessedes		ramo, ramo colorado, guayabo colorado	134,77
	155	224	*Diatenopteryx sorbifolia* Radlkofer	*Thouinia ornifolia* Gris	quebrachillo, sauquillo	256
*	156	225	*Diplokeleba herzogi* Radlkofer			374
	157	226	*Sapindus saponaria* L.		quillai, palo jabón, jaboncito, saponaria, casita	256
	158	227	*Serjania glabrata* Kunth			375
45			SAPOTACEAE			
	159	228	*Chrysophyllum gonocarpum* (Mart. & Eichler) Engler	*Sapota g.* Mart.& Eich.; *C. lucumifolium* Gris.	aguay	302,256,351
		229	*Chrysophyllum marginatum* (Hook. & Arn.) Radlk. **subsp.** *marginatum*	*C.maytenoides* Mart.; *C. grisebachii* (Hier.) Mez	lanza blanca, carapún, blanquillo colorado	303,136,351
*	160	230	*Pouteria gardneriana* (DC.) Radlk.	*Lucuma gard.* DC.		352

	161	231	*Sideroxylon obtusifolium* (Roem. & Schult.) Pennington **subsp.** *obtusifolium*	*Bumelia obtusifolia* Roem. &Schul.; *B. sartorum* Mart.	molle blanco, m. del monte, m.crespo, m.negro, horco-molle, chiri-molle, lanza colorada	93,136,351
46			SCROPHULARIACEAE			
*	162	232	*Basistemon silvaticus* (Herzog) Baehni & Macbr.	*Saccanthus silvaticus* Herzog		50
		233	*Basistemon spinosus* (Chodat) Moldenke	*Hassleropsis spinosus* Chod.; *Saccanthus violaceus* Herzog		50
47			SIMARUBACEAE			
	163	234	*Alvarodoa puberulenta* (Monachino) Sleumer	*A.amorphoides* Liebm. **var.** *puberulenta* Mon.	pichi blanco, tipilla	134,136,410
48			SOLANACEAE			
*	164	235	*Brunfelsia boliviana* Plowman		bella unión	358
		236	*Brunfelsia uniflora* (Pohl) D.Don	*Franciscea unifl.* Pohl	bella unión	357, h.s.
	165	237	*Cestrum lorentzianum* Grisebach	*C.calycinum* Willd.?; *C. viridiflorum* Hook.?	hediondilla	210?,134?,303,97
C	166	238	*Lycium cestroides* Schlechtendal	*Acnistus cestroides* (Schlech.) Miers	comida devíbora, ischivil, chile/i, tala churqui, chivil, talilla, etc.	134,256,60
	167	239	*Solanum granuloso-leprosum* Dunal	*S. riparium* Pers.; *S. verbascifolium* L.	tabaquillo, lata de pobre	302,303,136,319, 64,77

	168	240	*Vassobia breviflora* (Sendtner)Hunziker	*Acnistus brev.* Sendt.; *A.parviflorus* Gris.; *Dunalia b.*(Sen.)Sleum.	candelilla, chalchal de gallina, yuá, ischivil, palo negro, sacha perilla, pucancho, etc.	134,303,256,229, 77
49			STERCULIACEAE			
	169	241	*Ayenia subtilis* Cristóbal			128
*		242	*Ayenia tomentosa* L.			128
	170	243	*Byttneria oranensis* Cristóbal			129
*		244	*Byttneria scabra* L.	*B.salicifolia* Humb. & Bonpl. ex Schultes		129
		245	*Byttneria tucumanensis* Cristóbal			129
	171	246	*Melochia argentina* R.E. Fries	*M. argentina* Hassler		196
*	172	247	*Sterculia striata* St.-Hil. & Naud.			h.s.
50			TILIACEAE			
	173	248	*Heliocarpus popayanensis* Kunth		afata blanca	303,136
	174	249	*Luehea grandiflora* Mart. & Zucc.	[*L.speciosa* Willd.]	tabaquillo	256,130
51			ULMACEAE			
	175	250	*Celtis chichape* (Wedd.) Miquel	*C.tala* Gill. **var.***ch.* Pl.; *C.pubescens* (Kth) Spr. **var.***ch.* (Wedd.)Baehni		405
		251	*Celtis pubescens* (Kunth) Sprengel	*C.boliviensis* Pl.ex DC; *C. brasiliensis* Gard. ex Planchon	tala gateador, tala trepadora, tala de la selva	134,303,9,97, 405

		252	*Celtis spinosa* Sprengel	*C.tala* Gill. γ *gaudichaudiana* Plan.		405
	176	253	*Phyllostylon rhamnoides* (Poisson) Taubert	*Samaroceltis rhamnoides* Poisson	palo amarillo, palo de lanza, palo lanza, palo blanco	302,136,9,97
	177	254	*Trema micrantha* (L.) Blume		palo pólvora, afata colorada	303,136
52			URTICACEAE			
	178	255	*Urera baccifera* (L.) Gaud.		ortiga brava, ortiga colorada	136,97,256
		256	*Urera caracasana* (Jacq.)Gaud.ex Gris.		ortiga blanca, ortiga de monte	302,136
53			VERBENACEAE			
	179	257	*Aloysia triphylla* (L'Her.) Britton	*Lippia citriodora* (Ortega) Kunth	cedrón, yerba Luisa, yerba de la princesa	134,68
		258	*Aloysia virgata* (Ruiz & Pavón) Juss.	*A.urticoides* Cham.	niño-rupá	68
	180	259	*Lantana fiebrigii* Hayek			458
		260	*Lantana trifolia* L.			458
	181	261	*Lippia grisebachiana* Moldenke			458
		262	*Lippia suffruticosa* (Gris.) Ktze			458
54			ZYGOPHYLLACEAE			
C	182	263	*Porlieria microphylla* (Baill.) Desc., O'Don. & Lourt.		cucharero, palo cuchara, chucupí, guayacán, cuchupí	9, 97,256

5. PATTERNS OF DISTRIBUTION OF CHACO AND CAATINGAS SPECIES IN THE NEOTROPICS

5.1- Chaco endemics and other characteristic species of the Chaco:

In the previous chapter the woody and succulent species of the Chaco have been listed; 136 genera and 297 species occur in what is here understood as Chaco *sensu stricto* . Only eight genera are strictly endemic to the phytogeographical province, all of them monotypic: *Stetsonia* , *Setiechinopsis* , and *Castellanosia* in the Cactaceae, *Lophocarpinia* , *Mimozyganthus* and *Stenodrepanum* in the Leguminosae, and *Amphipetalum* and *Grahamia* in the Portulacaceae. Table 5.1 lists 92 species here regarded as exclusive to the Chaco, which represent *ca* . 31% of the total number of woody and succulent Chaco species. Distribution maps are given for 12 of these species: *Aspidosperma triternatum* , *Lophocarpinia aculeatifolia* , *Maytenus spinosa* , *M. vitis-idaea* , *Prosopis fiebrigii* , *P. kuntzei* , *P. ruscifolia* , *P. vinalillo* , *Schinopsis cornuta* , *S. quebracho-colorado* , *Tabebuia nodosa* and *Ziziphus mistol* (Figs. 5.1 to 5.12, respectively).

Some of the remaining species are virtually endemic to the Chaco since they extend only marginally into neighbouring provinces, such as *Aspidosperma quebracho-blanco* and *Schinopsis balansae* (Figs. 5.13 & 5.14), which are two of the most characteristic trees of the Chaco, but they extend to transitional communities in Mato Grosso do Sul (Prado et al., in press, b). Similarly, although *Prosopis affinis* is a typical chaquenian species, it extends as far east as to Rio Grande do Sul in Brazil or W Uruguay (Fig. 5.15). However, the Chaco shares the highest number of species with the Monte province of the arid west of Argentina (Sarmiento, 1972 & 1975; Solbrig, 1976). Some of these are of mainly chaquenian distribution but can also be important members of the Monte province (*sensu* Morello, 1958), such as *Geoffroea decorticans* (Fig. 5.16), which also extends to the Chilean Espinal and dry inter-andean valleys in Bolivia and Peru. *Prosopis alba* does not cross the Andes, but it extends to the Monte and dry valleys of Bolivia and Peru (Fig. 5.17), whereas *P. nigra* and *P. sericantha* only extend from typical Chaco into neighbouring Monte (Figs. 5.18 & 5.19). The low shrub *P. reptans* shows a more marked disjunction: whilst *P. reptans* var. *reptans* is largely restricted to the Chaco and it is absent from any

TABLE 5.1

GENERA ENDEMIC TO CHACO *S.S.*

	Nº of spp
CACTACEAE	
Castellanosia	1
Setiechinopsis	1
Stetsonia	1
FABACEAE	
Lophocarpinia	1
Mimozyganthus	1
Stenodrepanum	1
PORTULACACEAE	
Amphipetalum	1
Grahamia	1

SPECIES ENDEMIC TO CHACO

ANACARDIACEAE

1-*Schinopsis cornuta* Loes.

2-*Schinopsis heterophylla* Rag.& Cast.

3-*Schinopsis quebracho-colorado* (Schlecht.) Barkley & Meyer

APOCYNACEAE

4-*Aspidosperma triternatum* Rojas Acosta

? 5-*Vallesia glabra* (Cav.)Link.

ARECACEAE

6-*Trithrinax biflabellata* Barb. Rodr.

ASCLEPIADACEAE

7-*Marsdenia castillonii* Lillo ex Meyer

ASTERACEAE

8-*Flourensia campestris* Gris.

9-*Flourensia oolepis* Baker

10-*Heterothalamus alienus* OK.

BIGNONIACEAE

11-*Tabebuia nodosa* (Grisebach) Grisebach

BROMELIACEAE

? 12-*Bromelia hieronymi* Mez

? 13-*Bromelia urbaniana* (Mez) L.B.Smith

14-*Dyckia ragonesei* Castellanos

15-*Dyckia tweediei* Mez

CACTACEAE

16-*Castellanosia caineana* Cárd.

? 17-*Cereus comarapanus* Cárd.

? 18-*Echinopsis chacoana* Schütz

? 19-*Echinopsis minuana* Spegazzini

? 20-*Echinopsis schaferi* Br. & Rose

? 21-*Eriocereus guelichii* (Speg.)Berg

? 22-*Eriocereus martinii* (Lab.)Ricc.

? 23-*Eriocereus pomanesis* (Web.) ?

? 24-*Gymnocalycium capillensis* Hosseus

? 25-*Gymnocalycium ragonesei* Castellanos

26-*Monvillea cavendishii* (Monv.)Br.& Rose

27-*Monvillea spegazzinii* (Weber)Br.& Rose

? 28-*Opuntia brunnescens* Br. & Rose

29-*Opuntia quimilo* Schumann
? 30-*Opuntia retrorsa* Spegazzini
? 31-*Opuntia salagria* Castellanos
32-*Setiechinopsis mirabilis* (Speg.) Backg. ex de Haas
33-*Stetsonia coryne* (Salm-Dyck) Br.& Rose
34-*Trichocereus andalgalensis* (Web.)Hos.
35-*Trichocereus lamprochlorus* (Lem.) Br. & Rose
36-*Trichocereus spachianus* (Lem.) Ricc.

CAPPARIDACEAE

? 37-*Capparis retusa* Grisebach
38-*Capparis salicifolia* Grisebach
39-*Capparis speciosa* Grisebach
? 40-*Capparis tweediana* Eichler

CELASTRACEAE

41-*Maytenus spinosa* (Gris.) Lour.&O'Don.

CHENOPODIACEAE

42-*Atriplex eximia* Soriano

EUPHORBIACEAE

43-*Jatropha chacoana* Fernández Casas
44-*Jatropha matacensis* Castellanos

FABACEAE

CAESALPINIOIDEAE

45-*Bauhinia argentinensis* Burkart **var.** *argentinensis*
? 46-*Caesalpinia paraguariensis* (D.Parodi) Burkart
? 47-*Caesalpinia stuckertii* Hassler
48-*Lophocarpinia aculeatifolia* (Burk)Burk.
? 49-*Senna acanthoclada* (Gris.) Irwin & Barneby
50-*Senna chacöensis* (Bravo) Irwin & Barneby
? 51-*Senna spiniflora* (Burkart) Irwin & Barneby
52-*Stenodrepanum bergii* Harms

MIMOSOIDEAE

53-*Acacia curvifructa* Burkart
54-*Mimosa detinens* Benth.
55-*Mimozyganthus carinatus* (Gris.) Burkart
56-*Prosopis elata* (Burkart) Burkart
57-*Prosopis fiebrigii* Harms
58-*Prosopis hasslerii* Harms
59-*Prosopis kuntzei* Harms

60-*Prosopis pugionata* Burkart
61-*Prosopis rojasiana* Burkart
62-*Prosopis ruscifolia* Gris.
63*Prosopis vinalillo* Stuckert
PAPILIONOIDEAE
64-*Apurimacia dolichocarpa* (Gris.) Burkart
65-*Sophora linearifolia* Gris.

MALVACEAE
66-*Wissadula densiflora* R.E.Fries

MENISPERMACEAE
67-*Odontocarya asarifolia* Barneby

NYCTAGINACEAE
68-*Bougainvillea campanulata* Heim.
69-*Bougainvillea infesta* Gris.
70-*Bougainvillea praecox* Gris.

POLYGONACEAE
71-*Ruprechtia triflora* Gris.

PORTULACACEAE
72-*Amphipetalum paraguayense* Bacigalupo
73-*Grahamia bracteata* Gill. ex Hook. & Arn.

RHAMNACEAE
74-*Condalia montana* Castellanos
75-*Ziziphus mistol* Gris.

SANTALACEAE
76-*Acanthosyris falcata* (Mart. & Eichl.) Gris.

SIMARUBACEAE
77-*Castela coccinea* Gris.

SOLANACEAE
78-*Capsicum chacöense* A.T.Hunziker
79-*Lycium athium* Bernardello
80-*Lycium morongii* Britton
81-*Lycium nodosum* Miers
82-*Solanum argentinum* Bitt. & Lillo
83-*Solanum chroniotrichum* Morton

STERCULIACEAE
? 84-*Ayenia acalyphifolia* Gris.
85-*Ayenia cordobensis* (Hieron.) Hieron.
? 86-*Ayenia eliae* Cristóbal

? 87-*Ayenia lingulata* Gris.

? 88-*Ayenia o'donellii* Cristóbal

VERBENACEAE

? 89-*Aloysia gratissima* (Gill. & Hk.) Tr. **var.** *chacoensis* (Mold.) Botta

ZYGOPHYLLACEAE

90-*Bulnesia bonariensis* Gris.

91-*Bulnesia foliosa* Gris.

92-*Bulnesia sarmientoi* Lorentz ex Gris.

neighbouring phytogeographical area, Burkart (1976) cites this variety for a reduced area in Peru (Fig. 5.20); more strikingly, *P. reptans* Bentham var. *cinerascens* (A.Gray) Burkart is found on saline soils in Texas and adjoining Mexico (Burkart,*op .cit* .).

On the other hand, some typical Monte species extend deep into the Chaco (e.g. *Larrea cuneifolia* and *L. divaricata* , see Morello & Adámoli, 1974), or sometimes with more peripheral intrusions, e.g. *Bulnesia retama* , and *B. schickendantzii* in the Llanos district of the Chaco in La Rioja (Ragonese & Castiglioni, 1970), or *Monttea schickendantzii* and *Ramorinoa girolae* in very reduced areas of the Sierra Chaco (Ragonese & Castiglioni, *op .cit* .; Luti et al., 1979).

Some species are restricted in the Chaco to the mountainous areas of central Argentina in the Sierra Chaco where they are not only typical but also dominant, such as *Lythraea ternifolia* and *Schinopsis haenkeana* (Figs. 5.21 & 5.22). However, neither is exclusive to the Chaco; the former is occasionally found in the Monte province (Morello, 1958; Digilio & Legname, 1966) while the latter, in much less abundant populations than in the Sierra Chaco, is a member of the so-called Transitional Forests in NW Argentina and S Bolivia (Digilio & Legname, 1966; Ragonese & Castiglioni, *op .cit* .). Fig. 5.22 shows a cluster of dots for *Schinopsis haenkeana* in central Bolivia, based on herbarium material seen by the present author. According to Herzog's travel notes (1910 & 1912), which provide virtually the only data available for the vegetation of this sector, *S. haenkeana* seems to be both a member of deciduous forests on the eastern slopes of the Altiplano (Herzog, 1910) linked to the Argentine Subandean Piedmont Forests, and also member of communities in dry inner valleys (Herzog, 1912). The geographical area and floristic list coincides fairly well with Unzueta's (1975, p.101) 'monte espinoso subtropical', but he cites *S. cornuta* instead (probably a misidentification for *S. haenkeana*), of which there are no known collections for dry interandean valleys but only within Chaco *s.s.* (see Fig. 5.9, and Meyer & Barkley, 1973).

5.2- Caatinga endemics and other characteristic species of the Caatingas:

It has been proposed by both Rizzini (1963) and Andrade-Lima (1982) that the level of endemicity in the Caatingas is "too small to suggest

that the caatinga has its own unique flora which arose in the region" (Andrade-Lima, 1982, p. 247) at the specific and particularly the generic level. Andrade-Lima (1982) cited only three genera as endemic: *Fraunhoffera* , *Auxemma* and *Apterokarpos* . The latter is a somewhat contentious generic split from *Loxopterigium* (*apud* Barkley, 1962a), which was invalidly published by Rizzini (1975) since no basionym was cited. However, the number of endemic genera is in fact much higher since, as far as this author is able to ascertain from the available literature and herbarium material, there may be 12 endemic genera (and one endemic section) out of a total of 199 for the Caatingas (see Sect. 4.2), as follows: *Auxemma* (Boraginaceae; see map of Fig. 5.23), *Haptocarpum* (Capparidaceae), *Fraunhoffera* (Celastraceae; see map of Fig. 5.24), *Neoglaziovia* (Bromeliaceae), *Neesiochloa* (Graminae), *Arrojadoa* , *Stephanocereus* , *Tacinga* and *Zehntnerella* (Cactaceae), *Blanchetia* and *Telmatophila* (Asteraceae), and the recently described *Alvimiantha* of the Rhamnaceae (Grey-Wilson, 1978).

At the specific level the degree of endemicity is even more impressive, since within the Caatingas area *sensu* Andrade-Lima (1966a) there appear to be *ca* . 183 endemic and possibly endemic species (Table 5.2) out of a total of 437 species as ascertained from literature and herbarium material. This gives a level of endemicity of *ca* . 42% of the Caatingas species. Some examples of this kind of distribution are: *Bauhinia catingae* , *B. estivana* and *B. flexuosa* (Fig. 5.25), *Cordia dardani* and *C. leucocephala* (Fig. 5.26), *Cratylia mollis* and *C. nuda* (Fig. 5.27), *Hymenaea eriogyne* (Fig. 5.28), which appears to overlap slightly into the neighbouring Cerrados in W Bahia, *Maytenus rigida* (Fig. 5.29), *Mimosa adenophylla* , *M. glaucula* and *M. morroënsis* (Fig. 5.30), *Patagonula bahiensis* (Fig. 5.47), *Mimosa coruscocæsia* , *M. nothopteris* and *M. xique-xiquensis* (Fig. 5.37), *Alseis involuta* and what seems to be a new species in the genus *Simira* of the Rubiaceae (Fig. 5.31), the typical 'umbuzeiro' of the Caatingas *Spondias tuberosa* (Fig. 5.32), and the two endemics of the genus *Ziziphus* , *Z. cotinifolia* and *Z. joazeiro* (Figs. 5.33 & 5.34).

There are also some peculiar kinds of distributional patterns which deserve separate comment. *Commiphora leptophloeos* (sub *Bursera leptophloeos*) was assumed until very recently to be another

TABLE 5.2

GENERA ENDEMIC TO THE CAATINGAS

	Nº of spp
ASTERACEAE	
Telmatophila	1
Blanchetia	1
BORAGINACEAE	
Auxemma	2
BROMELIACEAE	
Neoglaziovia	1
CACTACEAE	
Arrojadoa	2
Stephanocereus	1
Tacinga	3
Zehntnerella	1
CAPPARIDACEAE	
Haptocarpum	1
CELASTRACEAE	
Fraunhoffera	1
EUPHORBIACEAE	
Manihot sect. *Glaziovianae*	7
POACEAE	
Neesiochloa	1
RHAMNACEAE	
Alvimiantha	1

SPECIES ENDEMIC TO THE CAATINGAS

ANACARDIACEAE

1-*Loxopterigium gardneri* Engler

2-*Spondias tuberosa* Arruda

APOCYNACEAE

3-*Aspidosperma riedelii* Müll. Arg. **subsp.** *oliganthum* (Wood.) Marc.-Ferr.

ARECACEAE

4-*Copernicia cerifera* (Arr.Cam.) Mart.

5-*Syagrus coronata* (Mart.) Becc.

6-*Syagrus microphylla* Burret

7-*Syagrus vagans* (Bondar) Hawkes

8-*Syagrus wedermannii* Burret

9-*Syagrus* x *matafome* (Bondar) Glassm.

ASTERACEAE

10-*Blanchetia heterotricha* DC.

11-*Telmatophila scolymastrum* Mart. ex Baker

BIGNONIACEAE

12-*Godmania dardanoi* (J.C.Gomes) Gentry

13-*Jacaranda irwinii* A.H. Gentry

14-*Tabebuia spongiosa* Rizzini

BOMBACACEAE

? 15-*Eriotheca parvifolia* (Mart.& Zucc.) Robyns

16-*Pseudobombax simplicifolium* Robyns

BORAGINACEAE

17-*Auxemma glazioviana* Taub.

18-*Auxemma oncocalyx* (Fr.All.) Taub.

19-*Cordia dardani* Taroda

20-*Cordia globosa* (Jacq.) Kunth

21-*Cordia leucocephala* Moricand

22-*Patagonula bahiensis* Moricand

BROMELIACEAE

23-*Aechmea eurycorymbus* Harms

24-*Bromelia laciniosa* Mart. ex Schult.

25-*Cottendorfia florida* Schultes f.

26-*Dyckia limae* L.B. Smith

27-*Dyckia pernambucana* L.B. Smith

28-*Encholirium spectabile* Mart. ex Schult.
29-*Hohenbergia catingae* Ule
30-*Neoglaziovia variegata* Mez

CACTACEAE

31-*Acanthocereus? albicaulis* Br. & Rose
32-*Acanthocereus brasiliensis* Br. & Rose
33-*Arrojadoa penicillata* (Gürke)Br.& Rose
34-*Arrojadoa rhodantha* (Gürke)Br.& Rose
35-*Austrocephalocereus dybowskii* (Gosselin) Backeberg
36-*Austrocephalocereus purpureus* (Gürke) Backeberg
37-*Brasiliopuntia bahiensis* (Britt. & Rose) Berger
38-*Cereus jamacaru* P.DC. non SD. ex Pfeiffer
39-*Discocactus bahiensis* Britt. & Rose
? 40-*Discocactus placentiformis* (Leh.) Sch.
41-*Discocactus zehntneri* Britt. & Rose
42-*Eriocereus adscendens* (Gürke) Berger
43-*Espostoa ulei* (Gürke) Buxbaum
44-*Leocereus bahiensis* Britt. & Rose
? 45-*Melocactus bahiensis* Britt. & Rose
46-*Melocactus horridus* Werdermann
47-*Melocactus oreas* Miquel
? 48-*Melocactus zehntneri* (Br.& Rose) Back.
49-*Opuntia palmadora* Britt. & Rose
50-*Pereskia aureiflora* Ritter
51-*Pereskia bahiensis* Gürke
52-*Pereskia stenantha* Ritter
53-*Pilosocereus catingicola* (Gür.)B.& Row.
54-*Pilosocereus chrysostele* (Vaup.) Byl. & Rowl.
55-*Pilosocereus glaucescens* (Lab.) Byl.& Rowl.
56-*Pilosocereus gounellei* (Web.) Byl. & Rowl.
57-*Pilosocereus piauhiensis* (Gürke) Byl. & Rowl.
? 58-*Pilosocereus tuberculatus* (Werd.)Byl.& Rowl.
59-*Pilosocereus zehntneri* (Br.& R.)Byl.& Rowl.
60-*Quiabentia zehntneri* (Br.& R.)Br.&Rose
61-*Stephanocereus leucostele* (Gürke) Berger
62-*Tacinga atropurpurea* Werdermann
63-*Tacinga braunii* Esteves
64-*Tacinga funalis* Britton & Rose

65-*Zehntnerella squamulosa* Britton & Rose

CAPPARIDACEAE

66-*Capparis jacobinae* Moric. ex Eichler

67-*Capparis yco* Mart.

68-*Haptocarpum bahiense* Ule

CELASTRACEAE

69-*Fraunhoffera multiflora* Mart.

70-*Maytenus rigida* Mart.

CHRYSOBALANACEAE

71-*Licania rigida* Bentham

COMBRETACEAE

72-*Combretum monetaria* Martius

? 73-*Combretum pisonioides* Taub.

74-*Combretum rupicola* Ridl.

ERYTHROXYLACEAE

75-*Erythroxylum betulaceum* Mart.

76-*Erythroxylum bezerrae* Plowman

77-*Erythroxylum caatingae* Plowman

78-*Erythroxylum maracasense* Plowman

79-*Erythroxylum macrochaetum* Miq.

80-*Erythroxylum petrae-caballi* Plowman

81-*Erythroxylum polygonoides* Mart.

82-*Erythroxylum pungens* O.E. Schulz

EUPHORBIACEAE

? 83-*Cnidoscolus bahianus* (Ule) Pax & Hoff.

84-*Croton argyrophylloides* Müll.Arg.

85-*Croton sincorensis* Mart.

86-*Croton sonderianus* Müll.Arg.

? 87-*Croton zehntneri* Pax & Hoffm.

88-*Ditaxis desertorum* (Müll.Arg.)Pax & Hoffm.

89-*Ditaxis malpighiacea* (Ule)Pax & Hoffm.

? 90-*Jatropha mutabilis* (Pohl) Baill.

91-*Manihot brachyandra* Pax & Hoffm.

92-*Manihot catingae* Ule

93-*Manihot dichotoma* Ule

94-*Manihot epruinosa* Pax & Hoffm.

95-*Manihot glaziovii* Müll.Arg.

96-*Manihot heptaphylla* Ule

97-*Manihot maracasensis* Ule
98-*Manihot pseudoglaziovii* Pax & Hoffm.
? 99-*Sapium argutum* (Müll.Arg.)Huber
? 100-*Sapium cicatricosum* Pax & Hoffm.
101-*Sapium sceleratum* Ridley

FABACEAE

CAESALPINIOIDEAE

? 102-*Bauhinia acuruana* Moric.
103-*Bauhinia catingae* Harms
? 104-*Bauhinia cheilantha* (Bong.) Steud.
105-*Bauhinia estivana* Wund. ined.
106-*Bauhinia flexuosa* Moric.
? 107-*Bauhinia pentandra* (Bong.) Vog. ex Steud.
? 108-*Caesalpinia bracteosa* Tul.
? 109-*Caesalpinia calycina* Benth.
? 110-*Caesalpinia laxiflora* Tul.
111-*Caesalpinia microphylla* Mart. ex Tul.
112-*Caesalpinia pyramidalis* Tul.
? 113-*Chamaecrista amiciella* (I&B)Ir.& Bar.
? 114-*Chamaecrista barbata* (Nees & Mart.) Irwin & Barneby
? 115-*Chamaecrista carobinha* (I&B)Ir.&Bar.
116-*Diptychandra aurantiaca* Tul. **subsp.** *epunctata* (Tul.) Lima, Carv. & Costa
117-*Hymenaea eriogyne* Benth.
? 118-*Peltogyne pauciflora* Benth.
119-*Senna acuruensis* (Bth.)I&B **var.***catingae* (Harms)I.&B. **var.** *interjecta* Ir. & Barn.
? 120-*Senna gardneri* (Benth.)Ir. & Barneby
? 121-*Senna martiana* (Benth.)Ir. & Barneby
? 122-*Senna rizzinii* Irwin & Barneby

MIMOSOIDEAE

123-*Acacia bahiensis* Benth.
? 124-*Acacia piahuiensis* Benth.
? 125-*Calliandra depauperata* Benth.
? 126-*Calliandra leptopoda* Benth.
? 127-*Calliandra squarrosa* Benth.
? 128-*Chloroleucon dumosum* (Benth.) Lewis
? 129-*Chloroleucon foliolosum* (Benth.) Lewis

130-*Mimosa adenophylla* Harms
131-*Mimosa coruscaesia* Barneby
132-*Mimosa glaucula* Barneby
? 133-*Mimosa misera* Benth.
134-*Mimosa morroënsis* Barneby
135-*Mimosa nothopteris* Barneby
? 136-*Mimosa pseudosepiaria* Harms
137-*Mimosa xiquexiquensis* Barneby sp. nov. ined.
138-*Parapiptadenia blanchetii* (Benth.) Vaz & M.P. Lima
139-*Parapiptadenia zehntneri* (Harms) M.P. Lima & Lima
? 140-*Piptadenia obliqua* (Pers.) Macbr.
? 141-*Piptadenia stipulacea* (Benth.) Ducke
? 142-*Pithecellobium diversifolium* Benth.
? 143-*Stryphnodendron piptadenioides* Marts.
PAPILIONOIDEAE
? 144-*Acosmium fallax* (Taub.) Yakovl.
145-*Coursetia rostrata* Benth.
146-*Coursetia vicioides* (Nees&Mart.) Benth.
147-*Cratylia mollis* Mart. ex Benth.
148-*Cratylia nuda* Tul.
149-*Dalbergia catingicola* Harms
150-*Dalbergia cearensis* Ducke
151-*Dalbergia decipularis* Rizz. & Matt.
? 152-*Discolobium hirtum* Benth.
? 153-*Lonchocarpus araripensis* Benth.
154-*Luetzelburgia andrade-limae* Lima
? 155-*Luetzelburgia bahiensis* Yakovl.
? 156-*Poecilanthe ulei* (Harms) Arr. & Rudd
157-*Pterocarpus ternatus* Rizzini
? 158-*Pterocarpus villosus* (Mart. ex Benth.)Benth.
? 159-*Pterocarpus zehntneri* Harms
160-*Riedeliella magalhaesii* (Rizz.)L.& Vaz
MALVACEAE
? 161-*Gaya aurea* St.-Hil.
? 162-*Herissantia crispa* (L.) Briz.
? 163-*Herissantia tiubae* (K.Schum.) Briz.
164-*Pavonia andrade-limae* H.Mont.
? 165-*Sida galheirensis* Ulbr.

? 166-*Wissadula contracta* (Link) R.E. Fries

? 167-*Wissadula patens* (St.-Hil.) Gürke

MYRTACEAE

168-*Campomanesia eugenioides* (Cam.) Leg. **var.** *desertorum* (DC.) Landrum

NYCTAGINACEAE

? 169-*Bougainvillea glabra* Choisy

OLACACEAE

170-*Ximenia coriacea* Engler

RHAMNACEAE

171-*Alvimiantha tricamerata* Grey-Wilson

172-*Ziziphus cotinifolia* Reiss.

173-*Ziziphus joazeiro* Mart.

RUBIACEAE

174-*Alseis involuta* Schum.

? 175-*Guettarda angelica* Mart. ex Müll. Arg.

176-*Simira* sp. Aublet

STERCULIACEAE

177-*Melochia betonicifolia* St.-Hil.

? 178-*Waltheria ferruginea* St.-Hil.

VELLOZIACEAE

179-*Xerophyta cinerascens* Roem. & Schult.

180-*Xerophyta plicata* (Mart.) Spreng.

VERBENACEAE

181-*Lantana caatingensis* Moldenke

? 182-*Lippia gracilis* Schauer

? 183-*Vitex gardneriana* Schauer

exclusive species of the Caatingas, where it is a frequent and typical contorted tree. However, Ratter (1987), Ratter et al. (1988b), and above all the taxonomic treatment of this species by Gillet (1979) have shown that there are isolated disjunctions away from the main center in the Caatingas. On calcareous ground in Corumbá (Mato Grosso do Sul) and in the Ilha do Bananal (Goiás) this tree is found in deciduous forests which have a floristic composition strongly related to that of the Caatingas in NE Brazil. Moreover, Ule collected this species in hills in Roraima state (Fig. 5.35). A different case is posed by *Hymenaea velutina* (Fig. 5.36), which whilst certainly a caatinga species (Lee & Langenheim, 1975) can also be found in cerradão in N Piauí and neighbouring Maranhão. This pattern seems to be followed by some other typical caatinga species which when extending into Piauí mix with cerrado elements in the 'carrasco' vegetation (see Sect. 3.4). Such is the case of *Piptadenia obliqua* (the 'catanduva' tree), *Cenostigma gardnerianum,* both characteristic species of the carrasco (Andrade-Lima, 1978; Emperaire, 1983), and sometimes *Luetzelburgia auriculata* (Lima, 1982). The famous and useful 'sabiá' of the sertão in Ceará is not an endemic either of that state nor even to the Caatingas as a whole (Fig. 5.37), contrary to Fernandes (1989); *Mimosa cæsalpiniifolia* has also been collected in Maranhão state, in the Amazon close to Manaus, and in the Atlantic Forest in Bahia (Lewis, 1987), although its occurrence in such areas is rather occasional and never as massive as in Ceará. Another similar case is *Mimosa exalbescens* (Fig. 5.30), which is not only a caatinga species but can also appear in secondary vegetation in Maranhão (Barneby, 1985).

5.3- Neotropical seasonal forests pattern:

In the Neotropics, from Mexico to Argentina, there is a discontinuous extension of deciduous and semideciduous forests which occur at low to mid-altitude and usually on mineral-rich soils, under a more or less strongly seasonal climate with a well-defined dry season of variable length. The similarity between the different fragments of this formation is not only physiognomical but also floristic. Thus, there are a number of woody species (which includes the most important Caatinga elements) whose pattern of distribution in the Neotropics closely follows the geographical dispersion of these seasonal forests, and many of them are exclusive to this formation.

5.3.1- Residual Pleistocenic Seasonal Formations Arc (Pleistocenic Arc):

A number of taxa seem to be restricted to a peculiar pattern of distribution in central South America which must have originated in the wet-dry climatic oscillations in the late Pleistocene. During the last dry period in South America, equivalent to the northern hemisphere Würm-Wisconsin glaciation, about 18,000 to 12,000 years ago, there appears to have been an expansion of semiarid vegetation in the continent (Damuth & Fairbridge, 1970; Ab' Sáber, 1977b; Brown & Ab' Sáber, 1979; Ab' Sáber, 1982). Ab' Sáber (1977b) postulates that during this period caatinga-like vegetation, which has an adaptive link to mineral-rich soils, may well have surrounded a central core area of cerrado vegetation in central Brazil, which in turn very probably extended into the Amazon region, whereas tropical rain-forests contracted everywhere into relatively small pockets in climatically more privileged areas. After the climax of the dry period there was a slow and gradual return to present-day wetter conditions during the last 12,000 years. The return of the more humid climate would be accompanied by leaching and acidification of soils, therefore fragmenting the originally much more widespread semi-arid vegetation.

Some isolated areas with caatinga-related vegetation can be found nowadays elsewhere in Brazil, in localities where rainfall is well above the 1,000 mm threshold (shown to represent one of the main limitant factors for the existence of this kind of vegetation, see Sect. 3.2), such as deciduous forests on calcareous outcrops (Ratter et al., 1978; Ratter, 1987; Ratter et al., 1988b; Prado et al., in press b), but in these cases it is the geopedological substratum that is determining their presence. They are on much more fertile ground than that surrounding the limestone outcroppings (e.g. mineral-poor cerrado soils, with toxic levels of aluminium), since the calcareous rock is permanently replenishing their shallow soil with essential elements. Thus, isolated refugia of the semiarid types of formations, left behind by the Pleistocenic corridors of caatinga-like vegetation (see discussion in Sect. 8.3), remain wherever suitable environmental conditions occur, i.e. on base-rich soils such as calcareous outcrops within the Cerrados, or in the Pantanal region.

A number of the woody species which are likely to have been involved in such expansion-retreat movements of the Pleistocene are today relevant members of the tropical and subtropical deciduous forest communities south of the Equator in South America, such as the Caatingas of NE Brazil, some semideciduous Planalto forests in São Paulo and Paraná states, the forests in the upper Uruguay river valley, most of the surrounding of the Paraguay-Paraná rivers system, the Serranías of Santiago and Chiquitos in SE Bolivia, the piedmont forests in the so-called Transitional areas in NW Argentina and SW Bolivia (running parallel to the Subandean mountains from Tucumán in Argentina to Santa Cruz de la Sierra in Bolivia), and more scattered outposts in semi-dry and dry Andean valleys in N Bolivia, throughout Peru and sometimes even reaching SW Ecuador. Some of these species are not only important members of these communities but also dominant in several cases.

One such case, and here taken as paradigm, is that of the Mimosoideae *Anadenanthera colubrina* var. *cebil* ('angico', 'cebil') (Fig. 5.38). There are three continuous distribution nuclei of this taxon in the Neotropics, from which discontinuous extensions radiate. The first and major nucleus consists of the Caatingas of NE Brazil, where the 'angico' is a very important and frequent tree. It is present in most of Andrade-Lima's vegetation units (see Sect. 3.4). Outwith the Caatingas, it has been reported in the 'brejos' from Pernambuco (Andrade-Lima, 1964b), particularly in the dry forests of the slopes of the 'serras', and in the so-called 'caatingas' in Maranhão state (Galvão, 1955). Eiten (1965, 1972) has repeatedly denied any link of this latter kind of vegetation to the true Caatingas province further east, although several of the vernacular plant names he mentioned are certainly employed for caatinga species ('angico', 'aroeira', 'pau d'arco', 'joá', 'mandacarú'). Bigarella et al. (1975) claim that disjunctions of Caatingas occur on the road Coroatá-Vargem Grande (Maranhão), while the exsiccatum marked on this map corresponds to Presidente Dutra, which is not too far south of these localities, and where caatinga-like vegetation can be assumed to exist. This NE Brazil nucleus for the 'angico' type of distribution is intermittently linked to the second nucleus, which occurs along the Paraguay-Paraná rivers system, by way of mesotrophic cerradão

woodlands in Goiás and Mato Grosso (Ratter et al., 1978), and in Mato Grosso do Sul (Ratter et al., 1988b; Prado et al., in press, b).

The second nucleus has a somewhat triangular shape with its northernmost apex on the axis Puerto Suárez-Corumbá (Bolivian-Brazilian border), a straight meridian side reaching south on the axis Resistencia-Corrientes in Argentina and thus parallelling the Paraguay river up to its confluence with the Paraná river, a latitudinal side eastwards from that confluence to the upper Uruguay river valley in Misiones (Argentina) and Santa Catarina (Brazil) and from here a diagonal side returning in NW direction to Pto Suárez-Corumbá. Thus, this nucleus includes nearly all of E Paraguay and a good deal of the western bank of the river Paraguay, that is a north-south strip parallel to the river and several kilometers inland in the geographical Gran Chaco region. Within this triangle *Anadenanthera colubrina* var. *cebil* is common but rarely dominant. It has been reported by Fiebrig (1933) along the western bank of the river Paraguay, by Tortorelli (1967) and Esser (1982) for several areas of E Paraguay, by Morello & Adámoli (1967) for eastern Formosa, and by Eskuche (1986) for NE Argentina in the Paranense phytogeographical province (Cabrera & Willink, 1980).

This second nucleus connects with the third one, located in SW Bolivia and NW Argentina, via the Santiago and Chiquitos hill ranges, forming a curved line uniting Corumbá to Santa Cruz de la Sierra. The flora of this region has scarcely been studied and even less collected, but Herzog (1910 & 1912) gives a fairly accurate impression of what the vegetation is like in the area. In the sector enclosed by this previous line and hills, by the western limit of the second nucleus, and by the north-south narrow strip of the third nucleus the true Chaco vegetation is encased. There are very few outposts of *Anadenanthera colubrina* var. *cebil* within the Chaco area (as is the case with most of the species with this pattern of distribution). The Cerro León records of this tree are not an exception to its absence from the plains of the Chaco *s.s.* , because the vegetation on the slopes of this tectonic horst (which comprises Silurian and Devonian rocks, as opposed to the æolian sediments surrounding the hill) shows strong links with the Subandean Piedmont Forests in NW Argentina (Ramella & Spichiger, 1989, *sub* Transitional Forests).

The third nucleus extends from Santa Cruz de la Sierra south to Tucumán and the sierras of E Catamarca in Argentina. This follows the piedmont area of the Subandean Mountains, which is the area of the so-called Transitional Forests, so-named because their floristic composition has been considered to be intermediate between that of the Chaco thorn forests and the upland subtropical rainforests (the 'Yungas' *s.s.*). *Anadenanthera colubrina* var. *cebil* was so important in the southern half of this nucleus in Argentina that Lillo (1919, as cited in Hauman, 1931, and Digilio & Legname, 1966) called it 'zona del cebil', but today there is little left of the original vegetation in this area. The northern remainder of the nucleus where the 'angico' occurs comprises the 'Palo blanco' forest, dominated by *Calycophyllum multiflorum* and *Phyllost ylon rhamnoides* , and which extends from mid-eastern Jujuy in Argentina to, presumably, Santa Cruz de la Sierra. *Anadenanthera colubrina* var. *cebil* is one of the five commonest members of both these forests (Cabrera, 1976, p. 7).

From this third nucleus this species, and the pattern of distribution dealt with here, becomes scattered along the NE-facing slope of the Andes in Bolivia and S Peru, i.e. from Santa Cruz to Cuzco, to even more scattered localities in dry interandean valleys such as those of the Apurímac, Huállaga and Marañón rivers (Weberbauer, 1936), finally reaching southern Ecuador in what corresponds to the 'Savannah and Dry Scrub vegetational types' (see map in Harling, 1979). The distribution of the typical variety, *Anadenanthera colubrina* var. *colubrina* , further extends the range of the species (Fig. 5.39) since although it occurs sympatrically with var. *cebil* in the southern area of the Caatingas in Bahia, and also in Misiones in Argentina, it is distributed allopatrically in Rio de Janeiro state and the Planalto forests of São Paulo and Paraná states. Altschul (1964) has argued cogently that the typical variety evolved from var. *cebil* , in which case var. *colubrina* has developed in wetter areas than those of its parental stock.

An important number of woody Caatingas species have a similar, sometimes virtually identical, distribution pattern to that of *Anadenanthera colubrina* var. *cebil* . For example, *Amburana cearensis* (Fig. 5.40) is a frequent, albeit not abundant, characteristic tree of the Caatingas even in the more shrubby types of communities, and it

occupies a similar niche in the 'Palo blanco' forest (3rd nucleus), whilst it is rather rare in the 2nd nucleus except for some dense populations on calcareous substrate on the Apa river region in Paraguay (Fiebrig, 1933; Tortorelli, 1967). It has also been reported for the Cerro León (Ramella & Spichiger, 1989), and it appears very occasionally in the Andean sector of this pattern of distribution; a collection from Acre state in Brazil should be noted. The tree *Astronium urundeuva* (Fig. 5.41) is usually an important member of whichever the community it occurs in: this is certainly the case for the arboreal caatinga, in which it is characteristic and dominant (Andrade-Lima, 1981), but it also extends into the shrubby caatinga as an isolated low tree (as does *Amburana cearensis* according to Egler, 1951). *Astronium urundeuva* is considered an indicator species of mesotrophic facies cerradão (Ratter et al., 1978) within the Cerrados area in central Brazil. It has been collected in the Cerro León, and it is very frequent in the Subandean Piedmont Forests of Argentina and Bolivia, but there are no records from the Andean dry valleys.

The beautiful tree *Enterolobium contortisiliquum* is usually conspicuous not for its frequency but rather for its size. Somewhat scarce in the Caatingas (Fig. 5.42), it has been reported for the agreste (Andrade-Lima, 1954) and arboreal caatinga (Andrade-Lima, 1975). In the Planalto forests its presence is recorded by collections and phytosociological works (Martins, 1979), and it is an important component of the vegetation on the banks of the Paraguay-Paraná system (Reboratti & Neiff, 1986; Prado et al., in press, a), and also of the Subandean Piedmont Forests (particularly in the 'Tipa-pacará' variant, see Sect. 2.3.8), but again is absent from the Andean area. *E. contortisiliquum* has also been collected in gallery forest within the Chaco (see map 5.42 and Morello & Adámoli, 1974), where it occurs with other non-chaquenian subtropical species, on the alluvial levees bordering the main rivers (Adámoli et al., 1972). *Pterogyne nitens* has a very similar distribution (Fig. 5.43) and is also reported for gallery forest and humidity dependant communities within the Chaco (Morello, 1967; Morello & Adámoli, 1974), but as a rather rare element of the latter. The species *Ruprechtia laxiflora* (Fig. 5.44) was originally described by Meisner (*in* Martius, 1855) from Blanchet exsiccata collected in the Caatingas (Cocucci, 1961), but it was not recorded subsequently in this area until recent collections by Harley et al. from around Camaleão in

Bahia. It was, however, abundantly collected in Paraguay and Argentina in both the 2nd and 3rd nuclei (Paraguay-Paraná system and Subandean Piedmont), where it is a very important element. The scandent shrub or treelet *Celtis pubescens* follows much more closely the *Anadenanthera colubrina* var. *cebil* pattern (although it is far less frequent in the Caatingas) and it reaches central Ecuador (Fig. 5.45) and is also recorded from Acre state in Brazil.

One of the most important and characteristic trees in the Caatingas is *Schinopsis brasiliensis* (Anacardiaceae). Engler (*in* Martius, 1876) recognized two varieties, var. *glabra* and the typical variety of this species. Meyer & Barkley (1973) subsequently considered the former variety to merit specific status, based on its lack of indumentum and larger leaflets when compared to var. *brasiliensis*. However, from numerous exsiccata this author has examined it would seem that although presence-absence of indumentum is a fairly consistent character, leaflet size is unreliable. A traditional view has been taken of *S. brasiliensis* , therefore, to include the two sympatric varieties, *brasiliensis* and *glabra* , and they have been mapped together (Fig. 5.46). This tree is not only present and abundant in the Caatingas, from where it extends into isolated localities in the Federal District of Brazil and in Minas Gerais (where it has been reported to form a dense community in a flood-prone area by Pinto, 1985), but also it is the dominant species in forests in Mato Grosso do Sul (Prado et al., in press, b). *Schinopsis brasiliensis* extends also from Corumbá to the west along the Santiago and Chiquitos ranges (Herzog, 1910), and there are abundant exsiccata from the humid slopes of the Andes in NW Bolivia, but it has not been recorded for Peru, where, however, it seems to be replaced by a similar and little known species, *S. peruviana* , which has been collected only twice (Fig. 5.46).

The genus *Patagonula* L. (Boraginaceae) seems to be endemic to the Pleistocenic Arc (Fig. 5.47). This genus comprises only two species: *P. bahiensis* is endemic to the Caatingas, whereas the type species *P. americana* has been collected or reported for the Planalto Forests in Paraná state in Brazil, the upper Uruguay river basin (Klein, 1972), E Paraguay, NE Argentina in subtropical forests from Misiones to the Eastern Chaco district (Cabrera, 1976; Lewis & Pire, 1981). It is also

the third most important species in the Subandean Piedmont Forests of NW Argentina and S Bolivia (Cabrera, 1976). Although *Patagonula* has not been reported from other areas of the Pleistocenic Arc, it would not be surprising for it to be encountered in the future in the rather poorly studied areas of Cerro León, the Santiago and Chiquitos ranges or south of Santa Cruz de la Sierra.

The species *Piptadenia viridiflora* poses a very interesting case since it is an important element of the Caatingas frequently reported in the literature (Fig. 5.48), while it is a relatively rare species in NW Argentina in the piedmont deciduous forests. Burkart (1952) cited this tree for Colombia and Venezuela (presumably for the dry Caribbean area), but no exsiccata or reference have been encountered to confirm this assertion. Both the species and the genus seem to be missing from the 2nd nucleus of this pattern of distribution, that is the Paraguay-Paraná system, but this may simply be due to a problem of taxonomic interpretation, since all previously considered *Piptadenia* species for this area have been transfered to other genera (*Anadenanthera* , *Goldmania* , *Parapiptadenia*). It is noteworthy that the species *Goldmania paraguensis* , endemic to this sector, is very close to section *Pityrocarpa* , to which Burkart (1952) referred *Piptadenia paraguensis* (Benth.) Lindm. (=*Goldmania paraguensis*), while Brenan (1955) transferred *Piptadenia viridiflora* to his genus *Pityrocarpa* .

There is only one collection of *Carica quercifolia* known from the Caatingas, from Irecê in Bahia (Badillo, 1971), and this would represent a very wide disjunct occurrence from the main, 'amphi-Chaco', area of distribution of this species (Fig. 5.49) if it was not for three additional isolated collections in Goiás, Minas Gerais and São Paulo states, which tenuously link the Bahian record to the 2nd nucleus of the Pleistocenic Arc. The rest of the distribution is divided into two more or less continuous zones separated by the Chaco plains. One corresponds to the Paraguay-Paraná system, extending eastwards along the upper Uruguay basin to include the Planalto forests, but also with an extension westwards into the Eastern Chaco. The second corresponds to the piedmont deciduous forests on the Subandean slopes. *Carica quercifolia* is also common in dry valleys between Andean ranges in NW Bolivia and S Peru.

The shrub *Combretum leprosum* is another typical caatinga species which follows relatively well the Pleistocenic Arc (Fig. 5.50). It is also common in Maranhão state in those areas suspected of having links with the Caatingas, and it has been collected in the river Paraguay valley and in Santa Cruz de la Sierra area, but seems to be missing from there to the south and north-west. The pattern followed by *Pouteria gardneriana* (Fig. 5.51) is somewhat more uncertain since although it is well recorded in the Caatingas and in the Paraguay-Paraná system, it is unclear whether it spreads into the Subandean Piedmont Forests apart from one collection in Santa Cruz in Bolivia.

The small tree *Tabebuia caraiba* , typically a cerrado species (Fig. 5.52), is also relatively common in the Caatingas of Pernambuco (Andrade-Lima, 1954 & 1960) and Bahia, and it can be found in the Amazon valley around Santarem. It has been frequently collected in the Paraguay river valley sector from Brazil to Argentina, while Ramella & Spichiger (1989) report it for cerrado-like communities on top of the plateau in Cerro León. This species also appears occasionally in central Bolivia, including a specimen collected near Santa Cruz de la Sierra, thus conforming somewhat to the Pleistocenic Arc here described, although the main core of *T. caraiba* distribution is the central Brazilian Cerrados area.

A rather different case is that of *Sterculia striata* (Fig. 5.53), which only marginally appears in tall, arboreal caatinga (Andrade-Lima, 1975; Ratter et al., 1978). It is much commoner in mesophilous forests within the Cerrados expanse or in mesotrophic cerradão (Ratter et al., 1978 & 1988b), but it shuns the poor soils of the Cerrados *s.s.*. It extends into the Amazon valley (Taroda, 1984) as well as to the river Paraguay area particularly on calcium-rich soils (Ratter et al., 1988b; Prado et al., in press, b), and its westernmost collections come from the area of Santa Cruz, thus overlapping a good deal with the *Tabebuia caraiba* distribution, albeit in different environments.

5.3.2- Tropical and Subtropical Seasonal Forests in South America:

Some caatinga species are widely distributed in South America but rarely appear away from deciduous seasonal formations. Such is the

case of *Aspidosperma cuspa* (Fig. 5.54), which has been collected in dry forests of Hispaniola and Martinique and it is a frequent tree in the dry Caribbean sectors of Colombia and Venezuela, countries in which it extends to some dry, interandean valleys. It reappears in SW Ecuador (Woodson, 1951), and at nearly the same latitude but on the opposite side of the continent in Rio Grande do Norte (NE Brazil). Rather an infrequent plant in the Caatingas, it can also be found scattered in the Cerrados of central Brazil, and finally in Paraguay on the rock outcroppings of the Cordillera de Altos (Marcondes-Ferreira, 1988). The taxonomically closely related *Aspidosperma polyneuron* (Fig. 5.55) coincides in part with the pattern of *A. cuspa* : it has also been collected in the western half of the dry Caribbean sector, and also in dry interandean valleys in Colombia, but has not been recorded, so far, from the eastern zone. No collections in Ecuador are reported, but it has been collected from N Peru in an area known to share a very similar kind of vegetation with SW Ecuador (Weberbauer, 1936; Harling, 1979). This N Peruvian locality is separated by some thousand kilometers from the next easterly records in central Bahia, Brazil. Thus, in the east, *A. polyneuron* occurs in the southern caatingas of Bahia, and then in a more or less continuous NE-SW arc spreading in mesophyllous forests in Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo and Paraná, extending from there to neighbouring Paraguay and a very reduced area in N Misiones (Argentina).

Another very interesting case is posed by the genus *Brunfelsia* (Solanaceae). Recently Plowman (1979) drew attention to the fact that *B. uniflora* forms a link between the older Andean species and the eastern Brazilian ones within section *Franciscea* (Fig. 5.56). It has been collected in N Venezuela, in Roraima (Brazil) and neighbouring Guyana (cf. *Commiphora leptophloeos* , Fig. 5.35), in the Yungas area of the eastern-facing slopes of the Andes in SW Bolivia and NW Argentina, to then reappear sporadically in the Caatingas and more abundantly in the Atlantic forests and Planalto forests in E Brazil. Two additional species are apparently derived from *B. uniflora* : *B. pilosa* and *B. australis* . The latter taxon, previously treated as a subspecies of *B. uniflora* , fills in the southernmost gap corresponding to the 2nd nucleus in the distribution of its mother species in Paraguay and NE Argentina (Fig. 5.57).

The unresolved taxonomic problem of the *Geoffroea striata / G. spinosa* complex (see comments in Burkart, 1949, and Lewis, 1987) provides another example of the Seasonal Forests Arc (Fig. 5.58), since in our experience the diagnostic characters provided by Burkart (1949) fail to clearly separate these alleged species. This complex is treated here as one polymorphic unit which, however, segregates very well from the other species of the genus, the typically but not exclusively chaquenian *G. decorticans* (cf. Fig. 5.16). The *G. striata / spinosa* complex appears in N Venezuela, E Ecuador and adjoining Peru, and in central Bolivia in the Yungas-like area of the Río Grande or Piraí, for the Andean related part, whereas in the lowlands there are essentially two nuclei: the Caatingas and the Paraguay-Paraná system. A very similar pattern is followed by the attractive *Ipomoea carnea* ssp. *fistulosa* (Fig. 5.59), including some Caribbean islands, N Colombia and Venezuela, the same sectors of Ecuador and Peru previously mentioned, and in riverine environments linked to the Subandean Piedmont Forests in NW Argentina but where the exsiccata might have escaped from cultivation (O'Donell, 1959b). In the east of the continent it occurs in the Caatingas and the Paraguay-Paraná system, and some odd appearances in the Amazon river valley area (around Santarem and Belém) have to be taken into account. This pattern is also followed in part by *Peltophorum dubium* (Fig. 5.60), which has been recorded for seasonal forests in Venezuela, but is more frequent in the SE of the continent, namely in the Caatingas, in mesophyllous forests in Minas Gerais, São Paulo and Paraná, in the upper Uruguay river valley in Santa Catarina, and it was frequently collected in E Paraguay. Once again this species is entirely absent from the Chaco, only to reappear in Yungas-like areas close to Santa Cruz de la Sierra in Bolivia.

The genus *Loxopterigium* in the Anacardiaceae presents five disjunct species in South America (Fig. 5.61). The scarcely known *L. gutierrizii* was collected only once in the Caribbean sector of Colombia, while *L. sagotii* is better known from the Guianas. The tree *L. huasango* appears only in seasonal semiarid to arid formations in coastal SW Ecuador and neighbouring Peru, whilst the caatinga woodlands of a small area of Piauí and Bahia contain the few recorded populations of *L. gardneri* (= *Apterokarpos gardneri*). Finally, *L.*

grisebachii is an important member of the Subandean Piedmont Forests in NW Argentina and S Bolivia, which separates Chaco vegetation from the rain and cloud forests of the Yungas. In this case, therefore, the allopatric species within a small genus together comprise the familiar distribution pattern of this Seasonal Forests Arc in South America.

A similar situation, but in this case with the component elements segregated as varietal taxa, occurs in *Senna spectabilis* (Irwin & Barneby, 1982). The var. *spectabilis* extends from coastal Venezuela to Andean valleys in the Mérida area of the same country and the Magdalena and Cauca river valleys in Colombia, to then reappear in seasonal formations in Ecuador and further south in dry valleys in the Peruvian Andes (Fig. 5.62). This variety is also a conspicuous member of the Yungas forests in Bolivia, and very particularly of the deciduous Piedmont forests in S Bolivia and NW Argentina where it is called 'carnaval'. As usual in this kind of distributional pattern this tree is entirely absent from the Chaco, only to reappear in E Paraguay. The other taxon, var. *excelsa* , is virtually restricted to the Caatingas in NE Brazil, where it is called 'canafístula'.

The shrub to small tree *Solanum granuloso-leprosum* also follows the tropical and subtropical seasonal forests pattern in South America (Fig. 5.63). It has been found in N Colombia and Guyana, disappearing completely from the Amazon but reappearing in the Caatingas of Bahia and Minas Gerais, continuing further south in mesophyllous forests in Rio de Janeiro, Paraná and Santa Catarina, and also extending into adjoining Paraguay - NE Argentina, particularly in the Austro-Brazilian Transitional Forest (see Sect. 2.3.3. a). As usual, it is absent from the Chaco but occurs in the eastern slopes of the Andes in NW Argentina and Bolivia.

This distributional pattern is also followed by another two-species-complex: *Cordia alliodora*/*C. trichotoma* (Fig. 5.64). Gibbs & Taroda (1983) studied this complex and concluded that both taxa should remain separate in view of the different kinds of heterostylous condition shown by plants of each species, together with differences in flower size, pollen grain size and mirmecophily. However, these taxa have had a confusing history and have been treated as conspecific by some authors,

whereas those who tried to differentiate them employed gross morphological characters (e.g. leaf indumentum) which are very variable within either species *sensu* Gibbs and Taroda (*op .cit* .). This complex seems to show a high degree of ecological plasticity, perhaps more important in *C. alliodora* , which extends from the semiarid Caribbean coast of Colombia and Venezuela, and the dry interandean valleys of these countries, but also occurs in the more humid Orinoco river valley and even in the Amazon. From western coastal Ecuador and Peru, the distribution follows the more characteristic dry valley systems to reach the Yungas area in Bolivia. The specimens collected in NW Argentina in the Subandean Piedmont Forests had been traditionally attributed to *C. trichotoma* , but from Gibbs & Taroda (*op .cit* ., Fig. 1) point of view they must be regarded as *C. alliodora* , based both on morphology and geographical range. The specimens on the eastern half of the complex distribution are nearly all considered *C. trichotoma* , which thus extends from the Caatingas, where this species can appear not only in the 'sertão' but also in the wetter hills ('brejos'), to mesophyllous forests on the Brazilian Planalto (Minas Gerais, São Paulo, Paraná and Santa Catarina), E Paraguay and NE Argentina.

Some species, such as *Platypodium elegans* (Fig. 5.65), which are more typical of the central Brazilian Cerrados vegetation, seem to shadow somewhat this distributional pattern. This species is a canopy tree in seasonal forest in Panamá (Porter, 1973), and it is also present in Venezuela, but it then disappears in the whole of north and central South America to reappear in the Caatingas, the Cerrados in Goiás, Mato Grosso, Minas Gerais and São Paulo, and further extends into E Paraguay and E Bolivia. *Astronium fraxinifolium* (fig. 5.66) is a tree found in N Colombia and Venezuela, and although it is absent from the Caatingas *s.s.* it has been recorded in semideciduous communities on higher ground within the general Caatingas area. In central Brazil, it has been considered one of the indicator species of mesotrophic cerradão by Ratter et al. (1977), a kind of deciduous forest linked to mineral-rich soils, and it extends also to E Paraguay and central Bolivia. There is a surprising collection of this species in the Cañadón Platanillos, in central Paraguayan Chaco, which must undoubtedly be linked to one of the watercourses which cross this region in a general E-W direction.

5.3.3- Amphitropical Seasonal Forests:

A number of species have a much more indistinct distribution pattern which can perhaps be referred to the extension of seasonal forests at both sides of the tropics. This sort of distribution is shown by a few caatinga species, although in each case they show fairly wide ecological plasticity and also occur in more humid habitats. One such is *Coutarea hexandra* (Fig. 5.67), which also occurs along the Amazon river, and also *Crateva tapia* (Fig. 5.68), which has been collected in the Amazon basin and also besides the ephemeral watercourses in the Caatingas. *Hymenaea courbaril* var. *courbaril* (Fig. 5.69), and the outstanding caatinga tree *Tabebuia impetiginosa* (Fig. 5.70) have similar distributions. Some such taxa are primarily restricted to seasonal habitats, such as *Myroxylon balsamum* (Fig. 5.71) and *Poeppigia procera* (Fig. 5.72), although these species also appear in the Amazon, or as in the case of *Phyllosthylon brasiliense* in the Brazilian Atlantic rainforest (see distribution of the genus in Fig. 5.73).

The distribution of the only three woody species (*Parkinsonia aculeata*, *Sideroxylon obtusifolium* and *Ximenia americana*) which are common to the Chaco and Caatingas follow this sort of pattern. *Parkinsonia aculeata* (Fig. 5.74) is a very widespread ruderal plant whose ecological amplitude includes the Pacific coastal desert of Peru and the arid Monte province of Argentina. *Sideroxylon obtusifolium* (fig. 5.75) seems to show the highest fidelity to the seasonal formations out of the nine amphitropical species shown here. Thus, and contrary to the rest of the species of amphitropical distribution which avoid temperate areas of Latin America, these latter species are exceptional in that they spread into areas such as Chaco, Monte, or even Patagonia in the case of *Ximenia americana* .

5.4- Other patterns of distribution:

A consistent group of caatinga species is relatively widespread in E South America but does not show the full sequence of links with other seasonal formations as do most of the cases considered above. However, a number of these species have a distribution which can be considered as a restriction to the eastern half of the Pleistocenic Arc. One such case is *Aspidosperma pyrifolium* (Fig. 5.76), which has also been collected and reported for Cerro León in Paraguay (Ramella &

Spichiger, 1989). It is a characteristic species of the Caatingas which spreads extensively into Minas Gerais, but then there is a disjunction with the populations on the river Paraguay (see map). There is also a puzzling exsiccatum from Faro (Marcondes-Ferreira, 1988), in the Pará state, a locality in a small sector of the Amazon valley where several other caatinga elements have also been collected (Andrade-Lima, 1959). The tree *Aspidosperma riedelii* has recently been treated by Marcondes-Ferreira (1988) as comprising two subspecies: ssp. *oliganthum* , a Bahian endemic, and ssp. *riedelii* with two disjunct populations in the Planalto forests of São Paulo and in central Paraguay (Fig. 5.77).

The valuable timber tree *Balfourodendron riedelianum* (Rutaceae) is a caatinga member (Fig. 5.78) extending south to the Planalto forests in São Paulo and Paraná states, along the upper Uruguay river valley, and reaching E Paraguay and NE Argentina. A similar case is that of *Hymenaea martiana* (Fig. 5.79), but it spreads from the Caatingas into the cerrado savannas in Goiás, the Federal District and Minas Gerais, as well as occurring in the forests in the Paraguay river area. *Machaerium acutifolium* is another cerrado species which occurs in the Caatingas (Fig. 5.80) and extends south into the Mata Atlântica in Rio de Janeiro, isolated 'campo' areas in Minas Gerais and São Paulo, and in forests in E Paraguay. The soft-wooded tree *Phytolacca dioica* has been relatively recently collected in the caatinga of Campo Formoso, Bahia (see specimen at K), and its presence there has been considered a proof of ancient floristic links between the Caatingas and the rest of this species distribution in South America via climatic changes (Andrade-Lima, 1982). This species is a common member of subtropical forests in the Paraguay-Paraná system (e.g. in the Austro-Brazilian Transitional forest), and extends eastwards through Planalto forests to coastal rainforests in Santa Catarina (Fig. 5.81). Some other more infrequent caatinga species extend only to the coastal rainforests of E Brazil, such as *Alseis floribunda* (Fig. 5.82) which is disjunct in coastal Rio de Janeiro, Paraná and Santa Catarina, as is *Astronium concinnum* (Fig. 5.83).

There is also a group of woody species which are entirely restricted to either the 2nd or 3rd nuclei (or both) within the Pleistocenic Arc (see sect. 5.3.1). The monotypic genus *Athyana* (Sapindaceae) is

endemic to the seasonal Subandean Piedmont forests of NW Argentina and S Bolivia (Fig. 5.84). Likewise, the monotypic genus *Diatenopteryx* (also Sapindaceae) occurs in both nuclei, leaving a large blank in the middle for the Chaco, and it extends into the Planalto forests and along the upper Uruguay (Fig. 5.85). In the ditypic genus *Diplokeleba* one species, *D. floribunda* , is abundant on the Paraguay-Paraná system, while the other, *D. herzogii* , is known only from the type collection in Cabezas, Bolivia (Fig. 5.86), most likely from the deciduous forests frequent in that area (Coro, 1956). Similarly distributed is *Ziziphus oblongifolius* (Fig. 5.87), a very frequent shrub in the north of the Paraguay-Paraná system (Prado et al., in press, b), and cited by Herzog (1910) for Bolivia and Escalante (1946) for Orán in Salta (Argentina).

The elegant Rubiaceous tree *Calycophyllum multiflorum* is the dominant and characteristic species of the 'Palo blanco' forest in the Piedmont of the Subandean chains (Fig. 5.88), to which it gives its vernacular name, and it is also common in the river Paraguay area and in the Cerro León (Ramella & Spichiger, 1989). Some isolated populations of *C. multiflorum* have been occasionally found within the Chaco *s.s.* (Castellanos, 1958; Morello, 1967; Morello & Adámoli, 1974), where it is likely they occur in the remains of a previously more expanded seasonal forest in the Pleistocene. Three other species can be considered to be confined to the Paraguay-Paraná system: *Astronium balansae* (Fig. 5.83), *Maytenus ilicifolia* (Fig. 5.89), the latter reaching Santa Catarina to the east, and *Ziziphus guaranitica* (Fig. 5.90).

Finally, it is necessary to consider the distribution of three caatinga species which seem to link with Amazonia, or at least to wet tropical formations. One such is *Albizia polyantha* (Fig. 5.91), which extends from the Guianas and Ilha de Maracá (Lewis & Owen, 1989), to the Amazon river valley and tributaries, and to the Caatingas, the Paraguay-Paraná system and Cerro León. The distribution of this species seems to be associated with permanent watercourses except in the Caatingas. *Aspidosperma discolor* appears in the Venezuelan Guayana and the Guianas, has been profusely collected in the lower and middle Amazon river valley and in the Rondônia state, but it is also frequent in Bahian caatinga and in a central area of the Cerrados (Fig. 5.92). *Couepia uiti* (Chrysobalanceae) is essentially an Amazonian

element, but via gallery forest it extends within the Cerrados and Caatingas (Fig. 5.93).

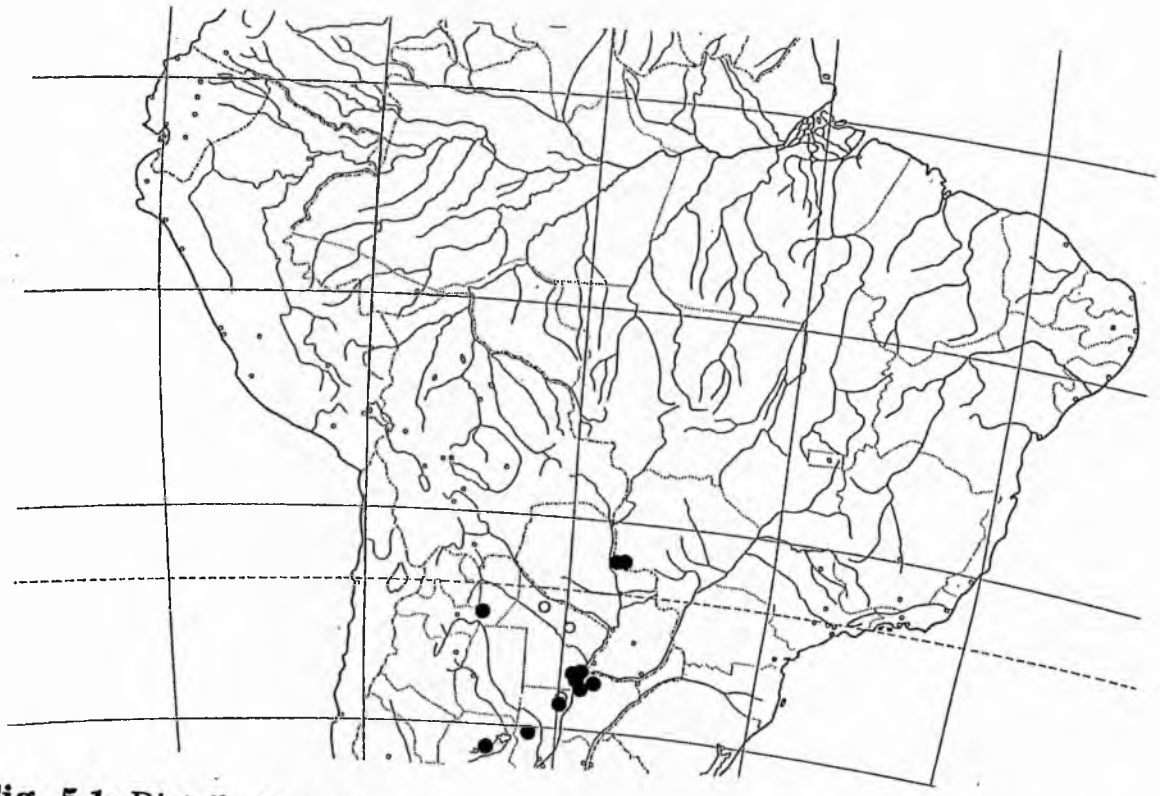
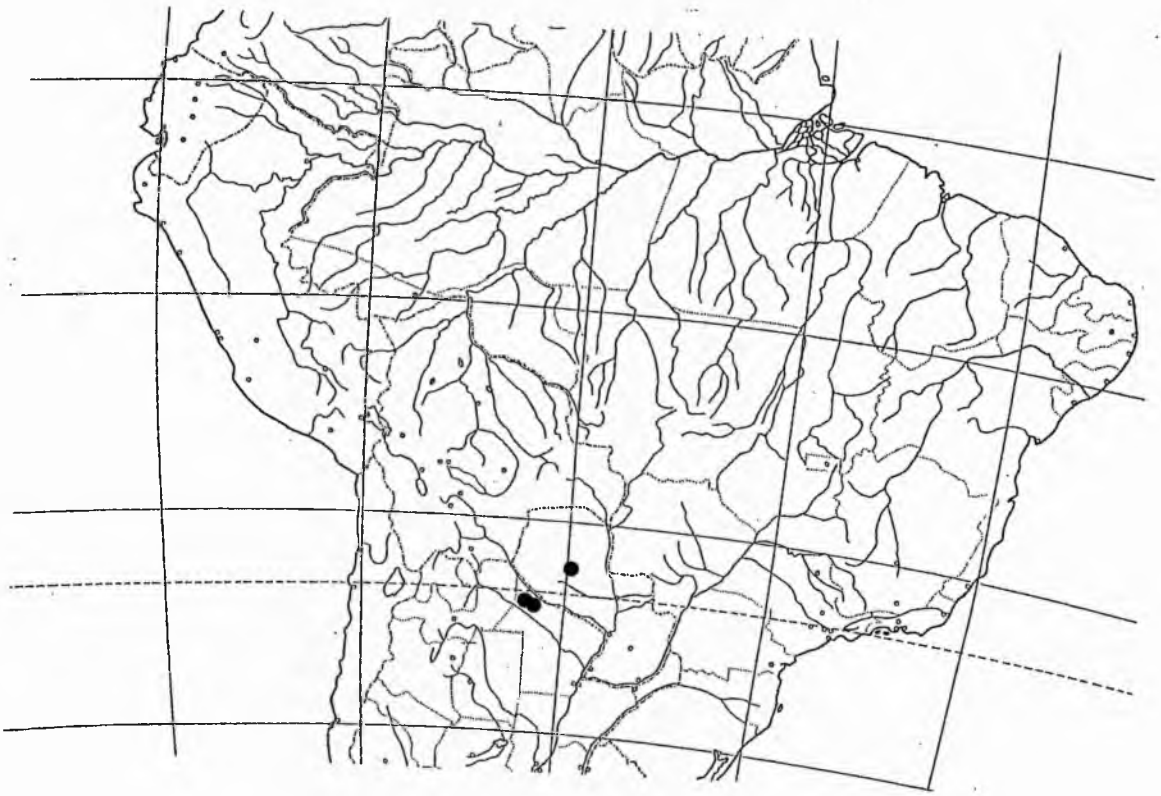


Fig. 5.1: Distribution map of *Aspidosperma triternatum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.2: Distribution map of *Lophocarpinia aculeatifolia*.



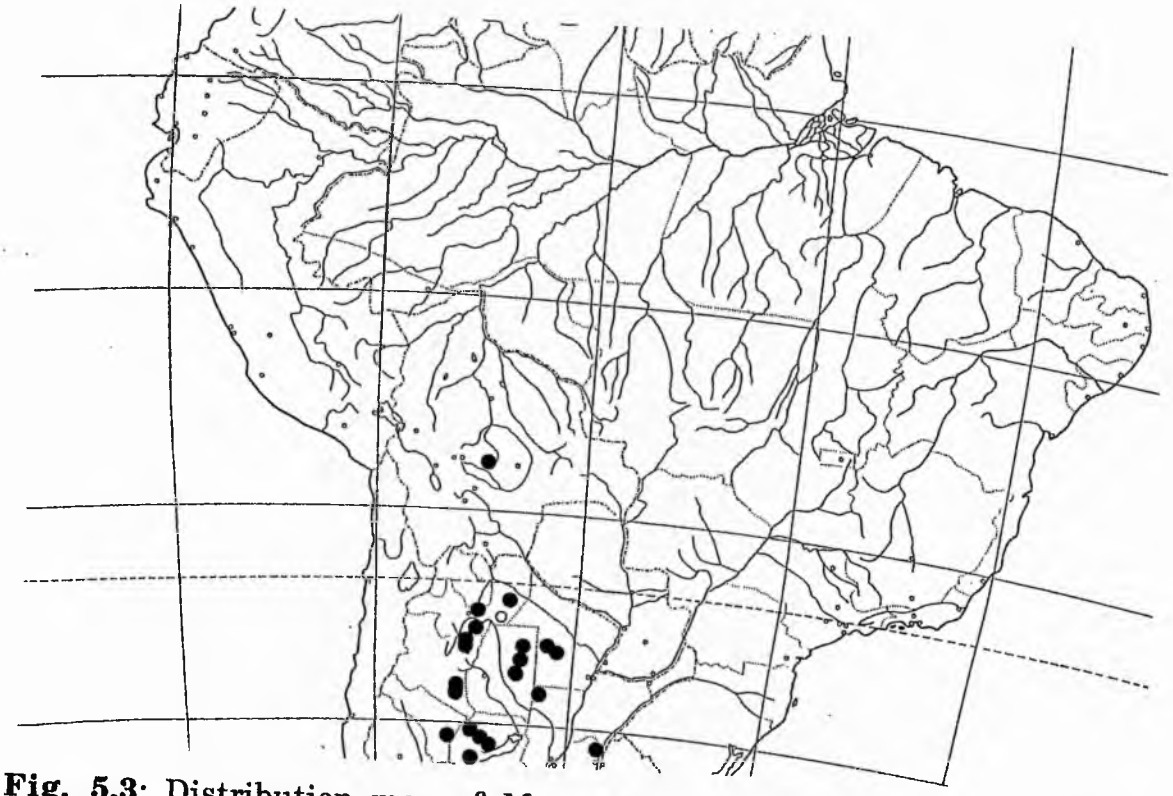
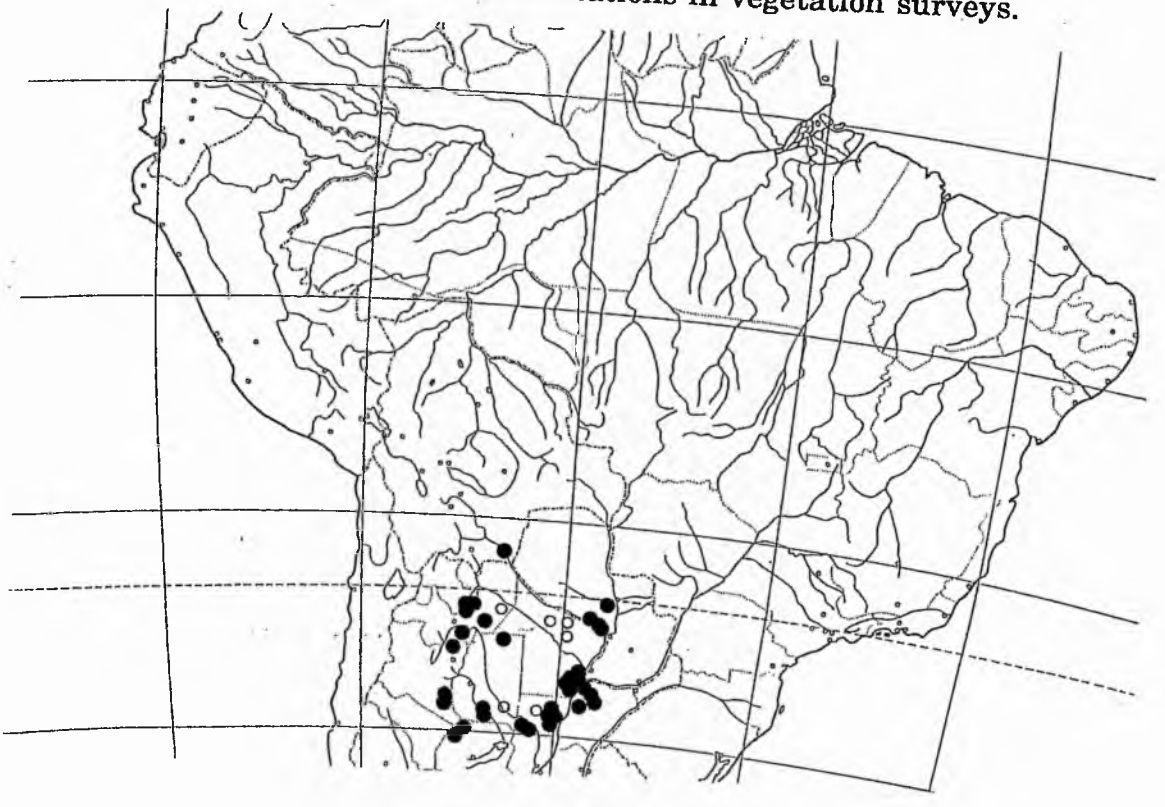


Fig. 5.3: Distribution map of *Maytenus spinosa*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.4: Distribution map of *Maytenus vitis-idaea*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



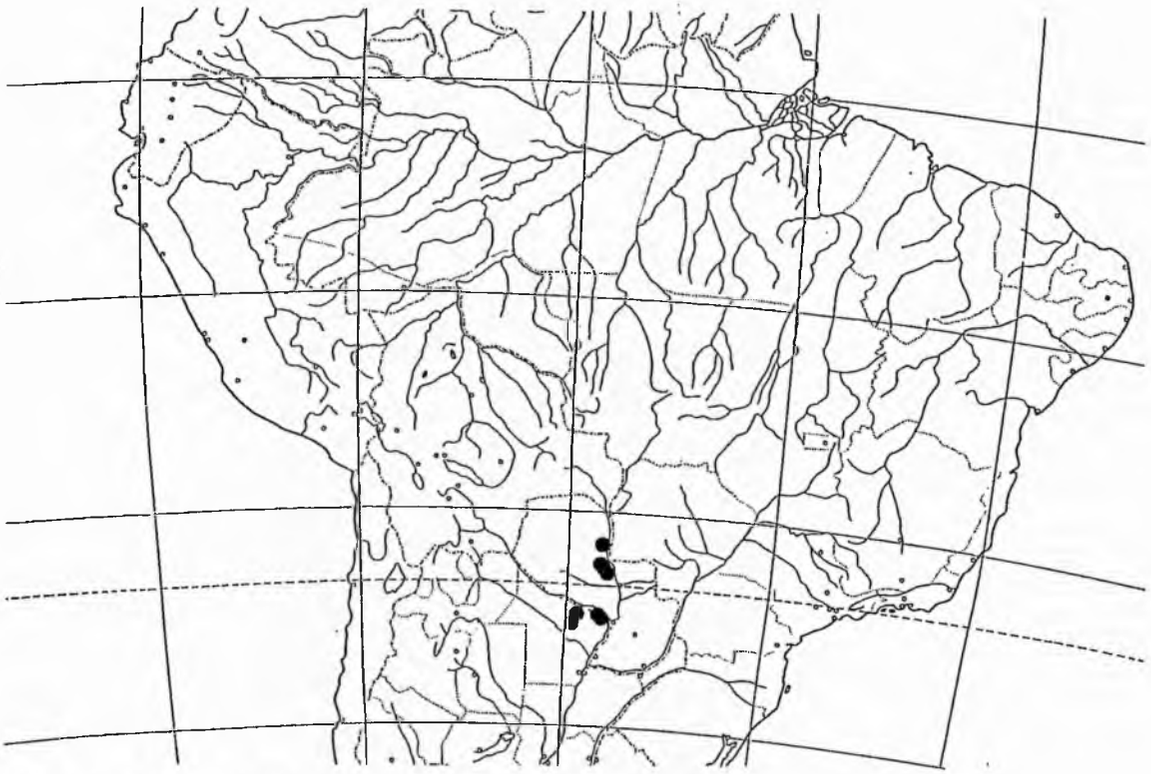
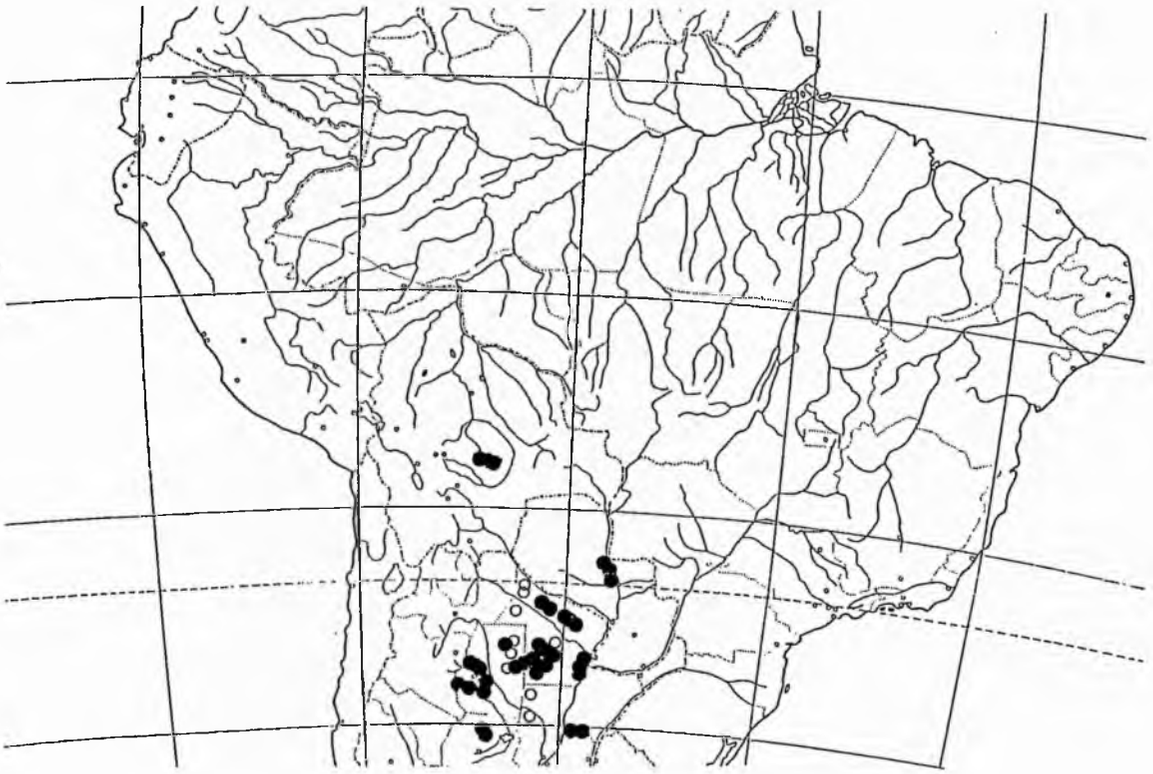


Fig. 5.5: Distribution map of *Prosopis fiebrigii*.

Fig. 5.6: Distribution map of *Prosopis kuntzei*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



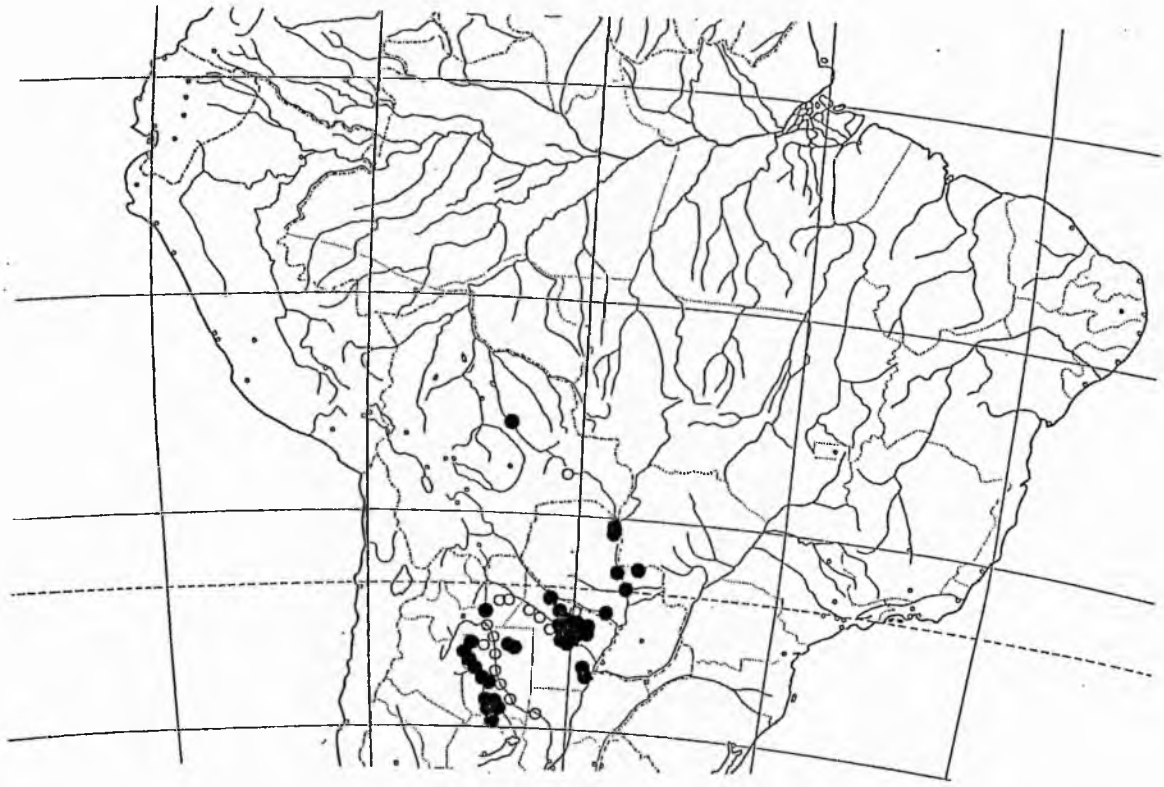
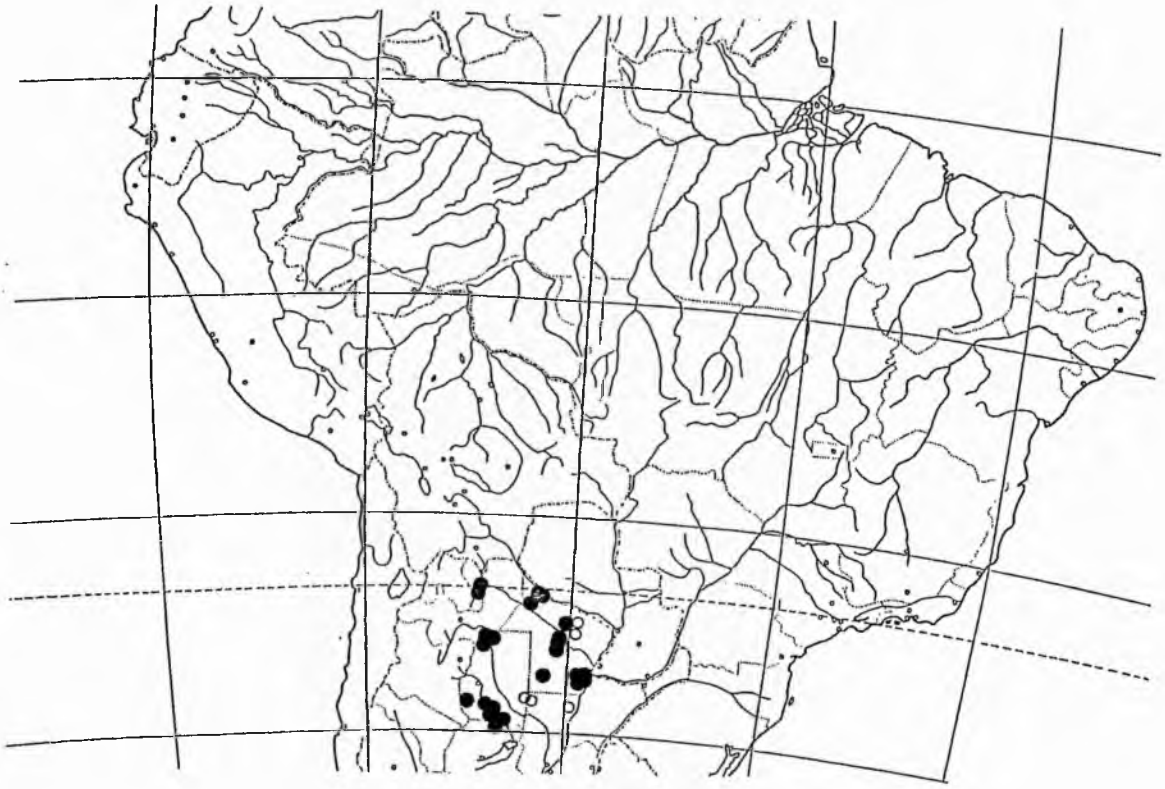


Fig. 5.7: Distribution map of *Prosopis ruscifolia*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.8: Distribution map of *Prosopis vinalillo*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



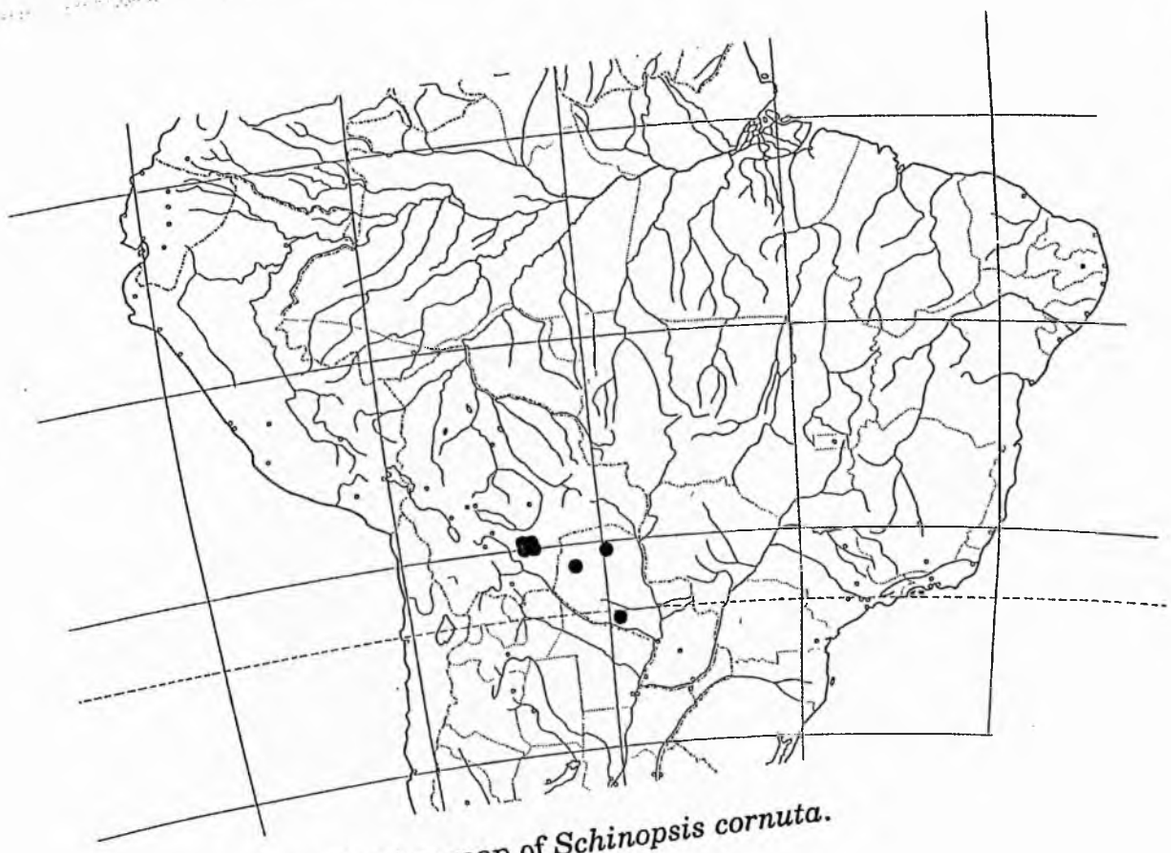


Fig. 5.9: Distribution map of *Schinopsis cornuta*.

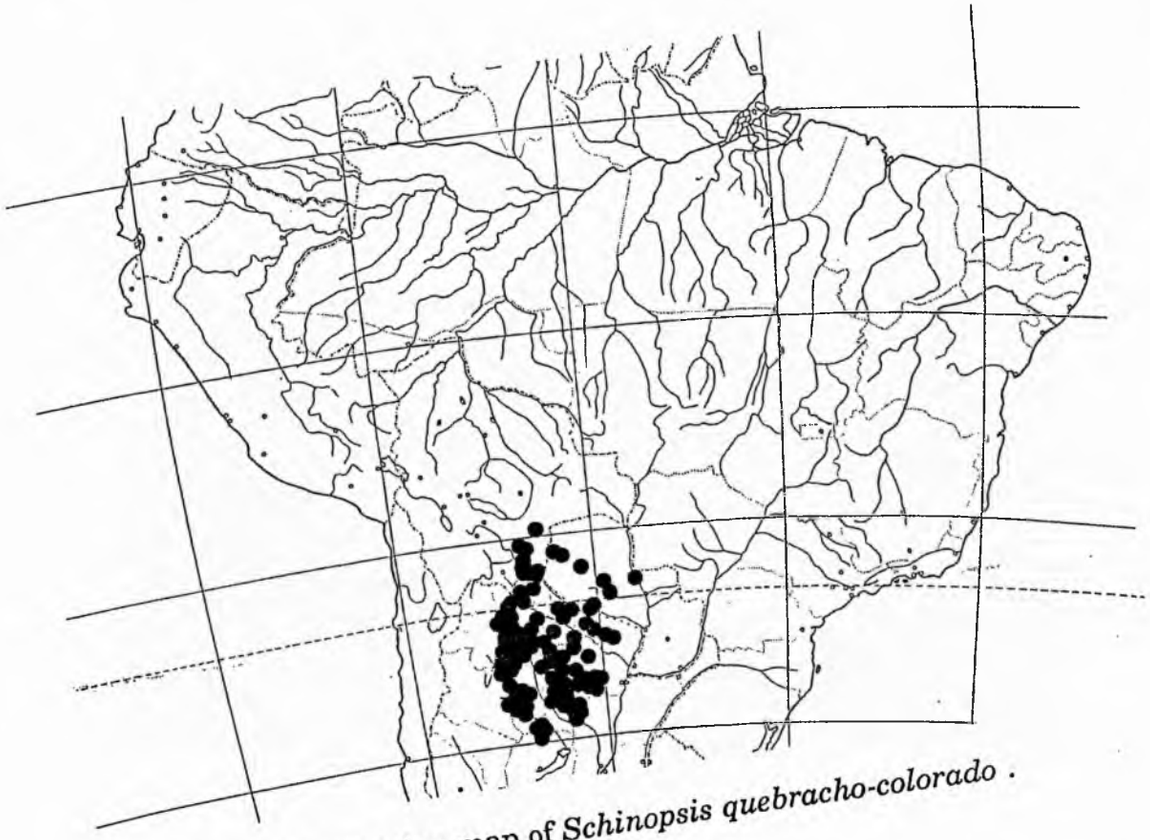


Fig. 5.10: Distribution map of *Schinopsis quebracho-colorado* .

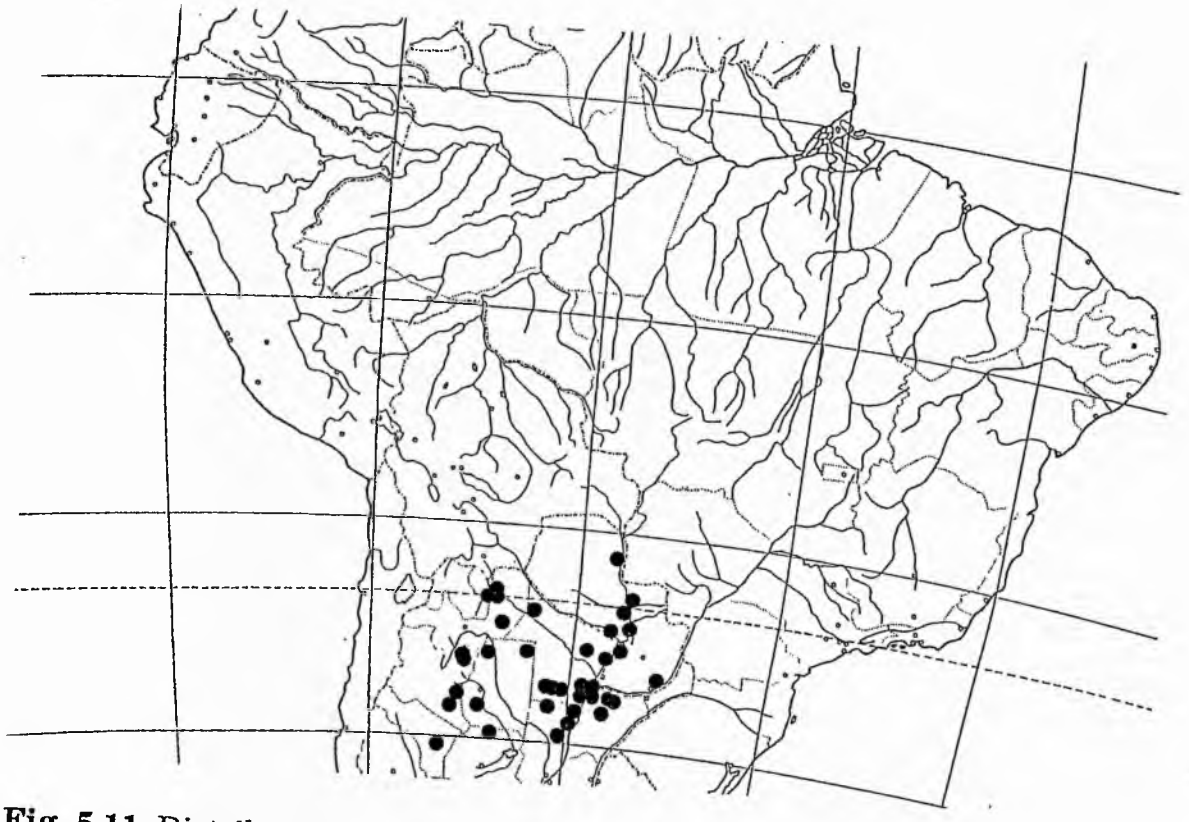
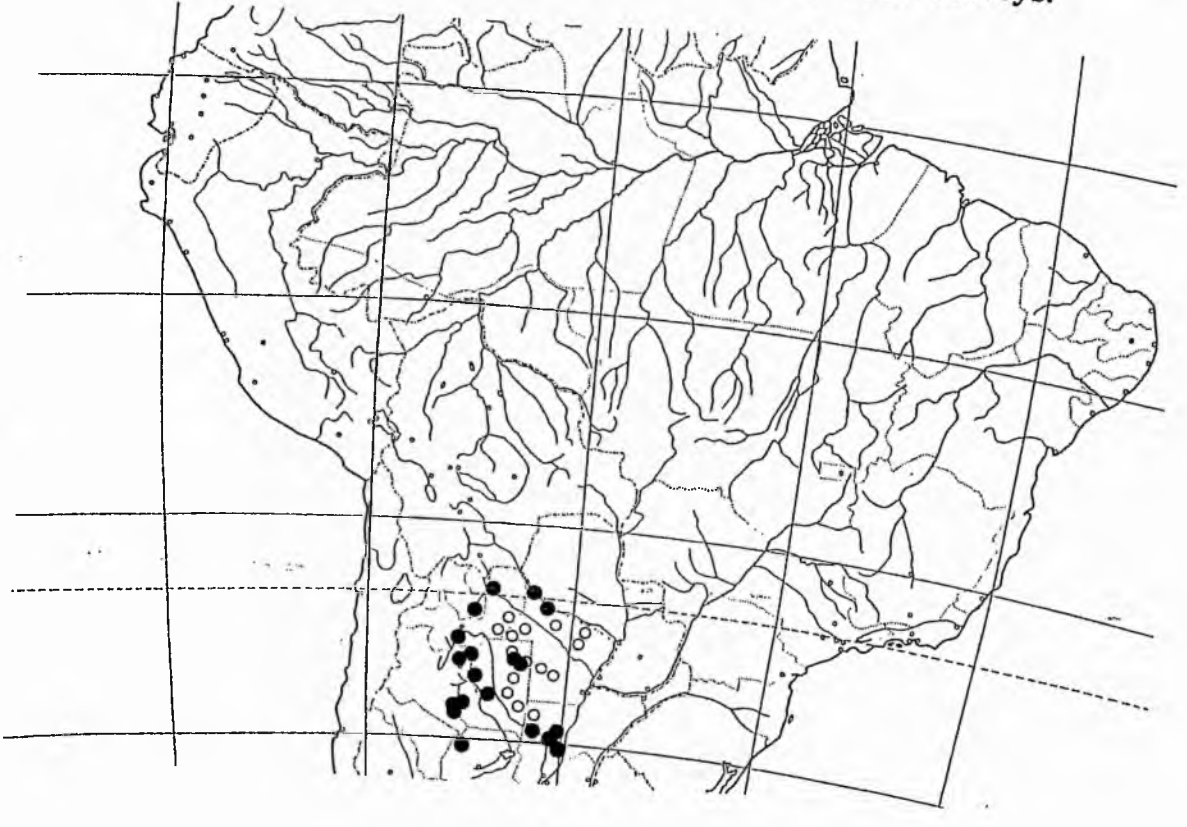


Fig. 5.11: Distribution map of *Tabebuia nodosa*.

Fig. 5.12: Distribution map of *Ziziphus mistol*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



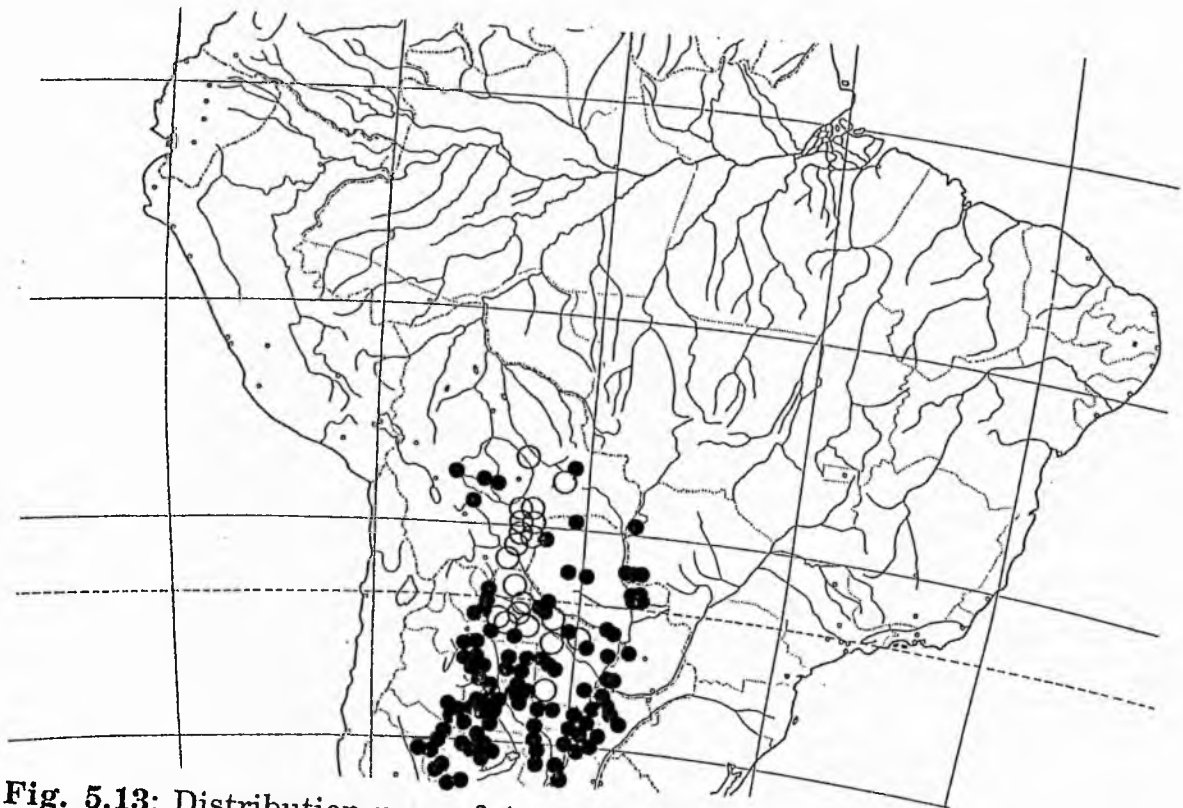
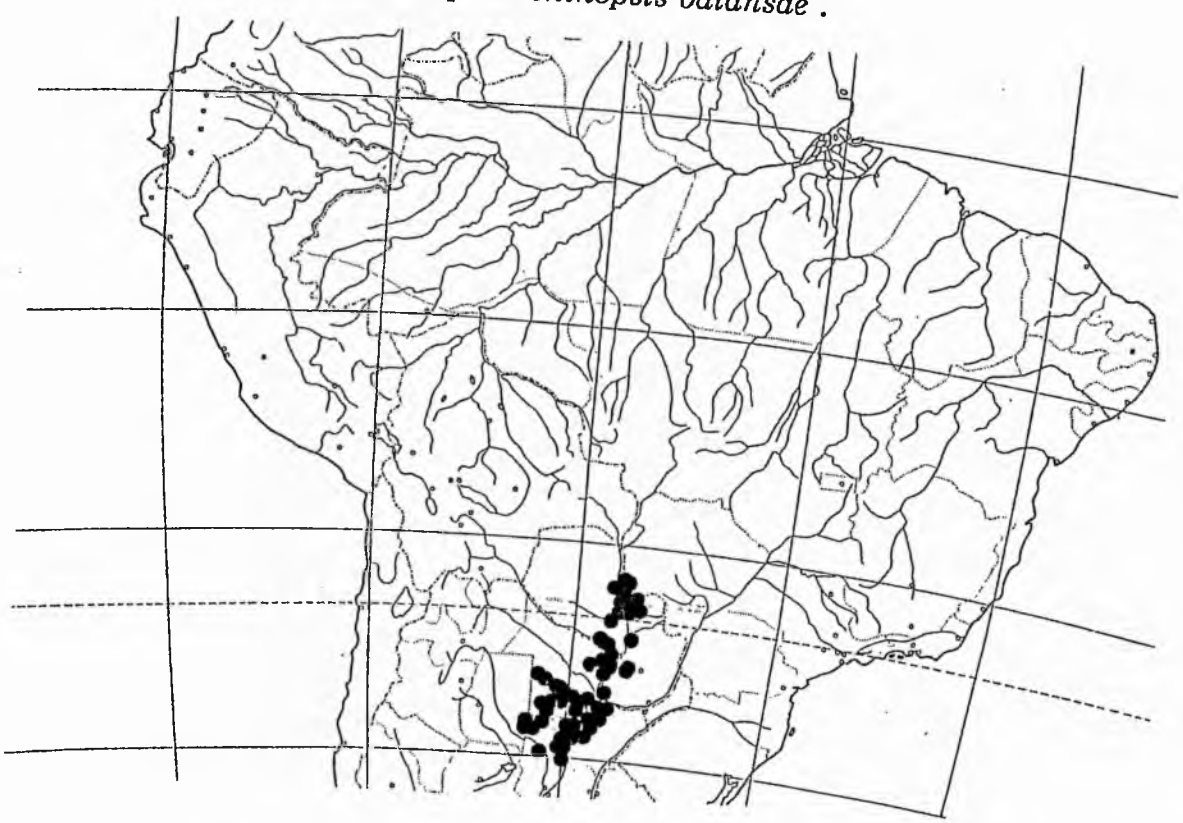


Fig. 5.13: Distribution map of *Aspidosperma quebracho-blanco* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.14: Distribution map of *Schinopsis balansae* .



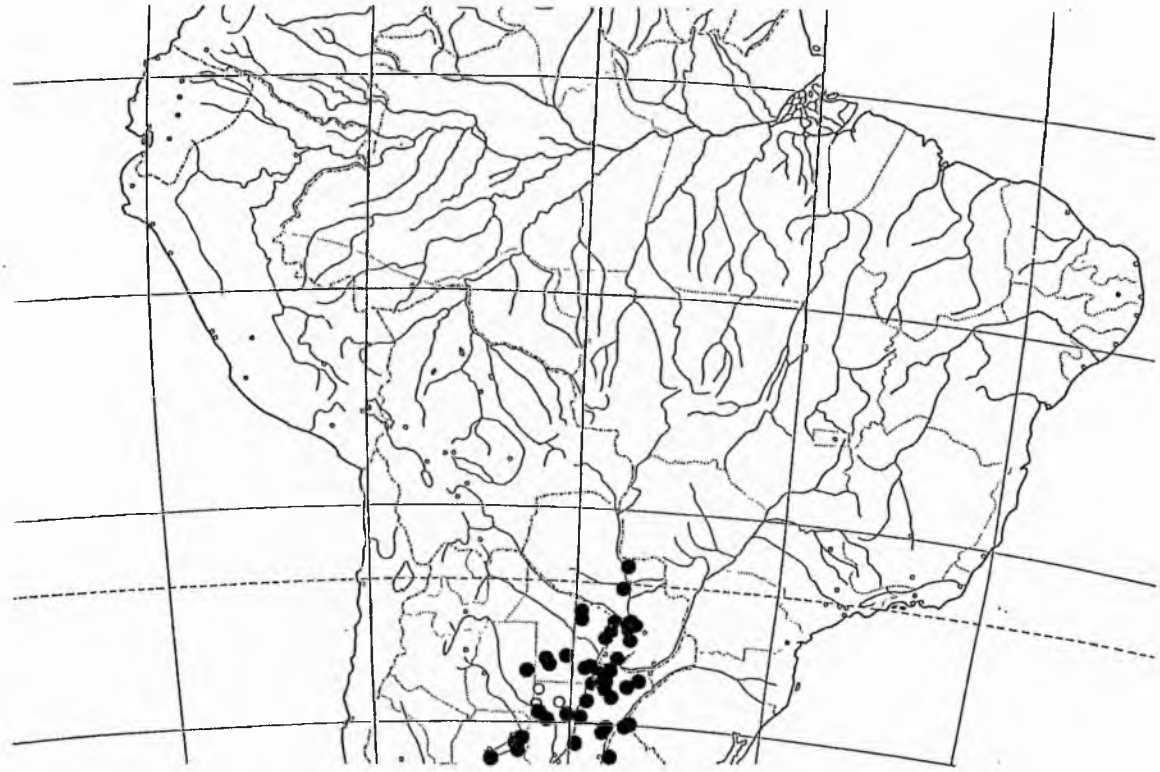
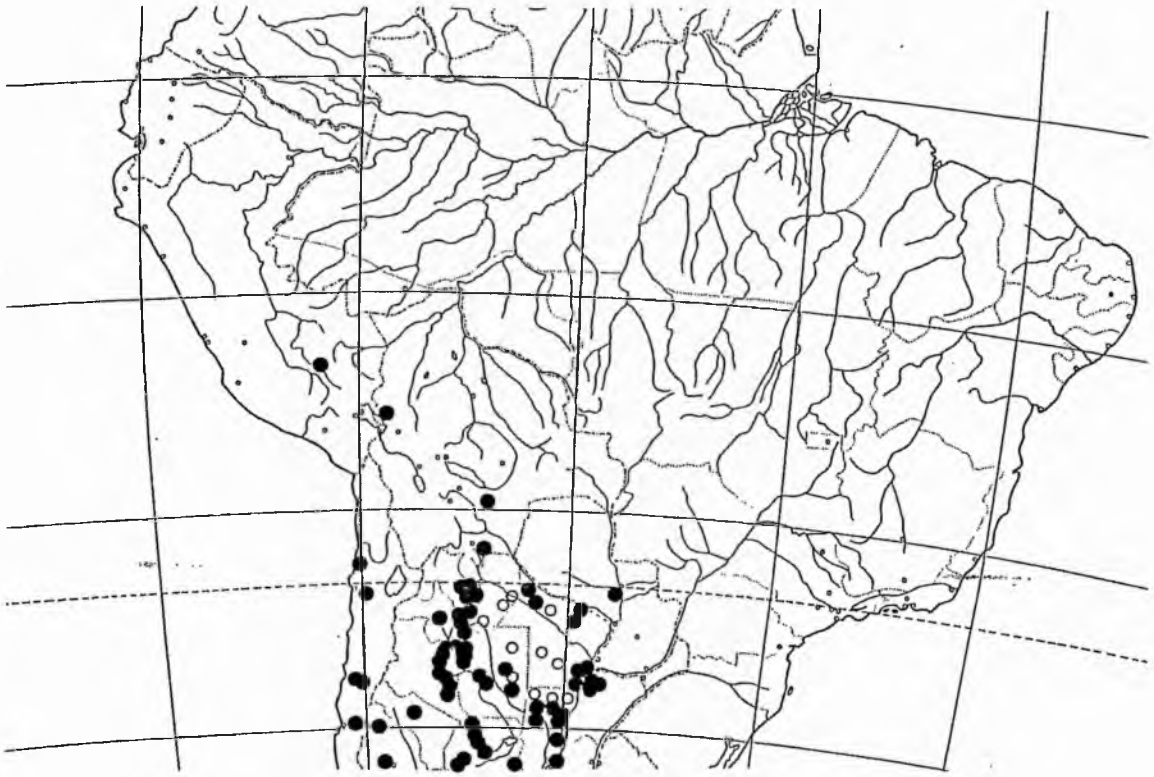


Fig. 5.15: Distribution map of *Prosopis affinis* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.16: Distribution map of *Geoffroea decorticans* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



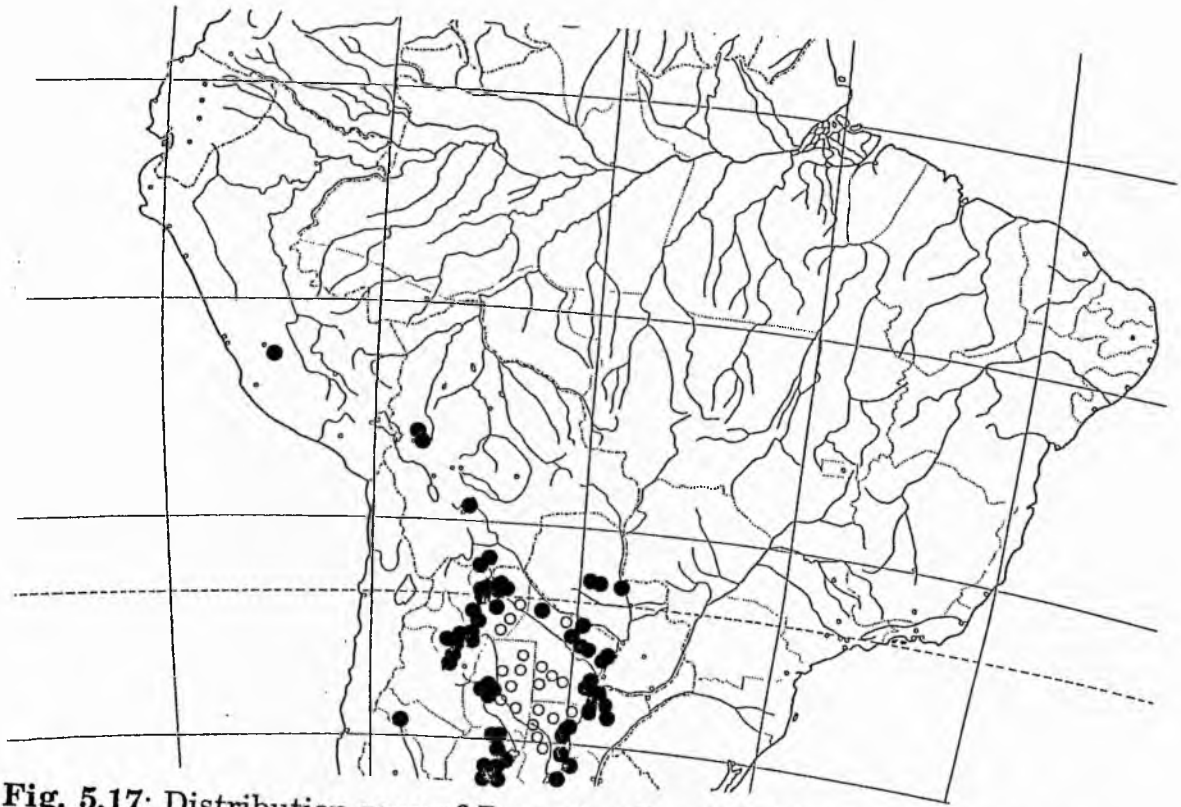
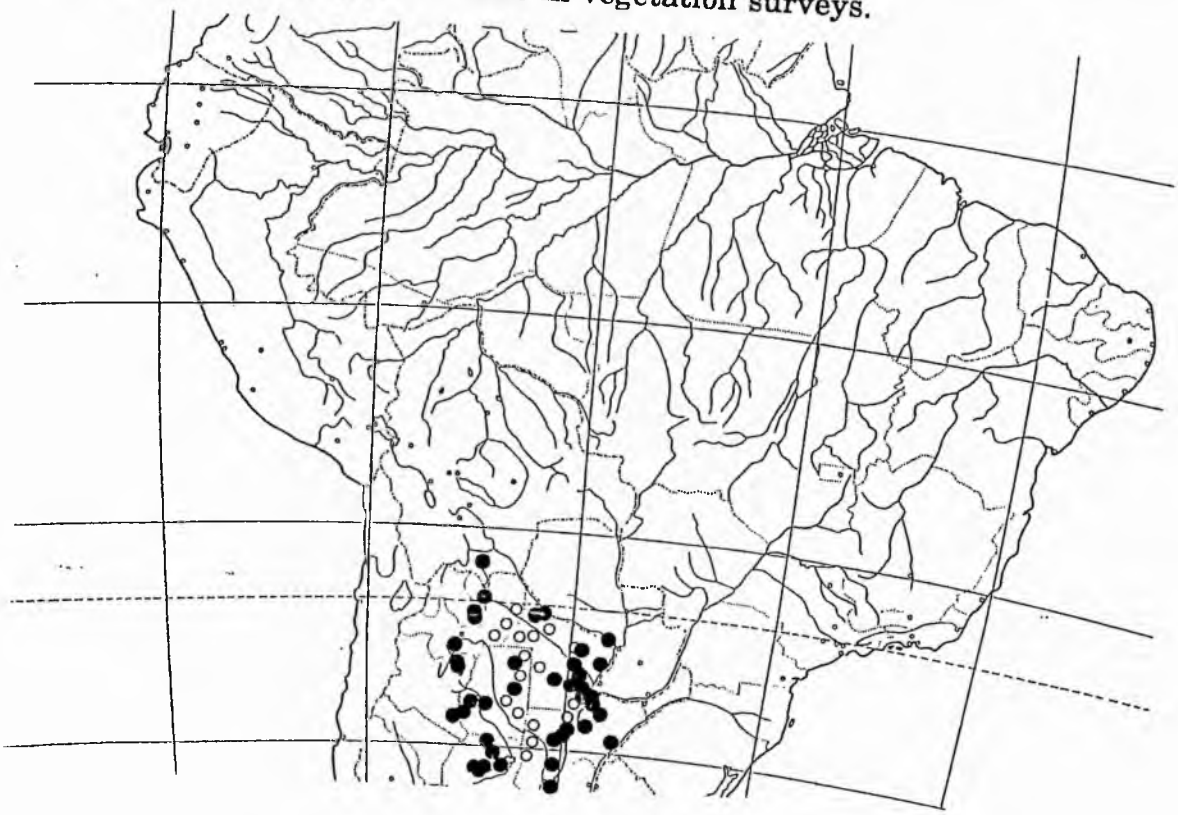


Fig. 5.17: Distribution map of *Prosopis alba*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.18: Distribution map of *Prosopis nigra*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



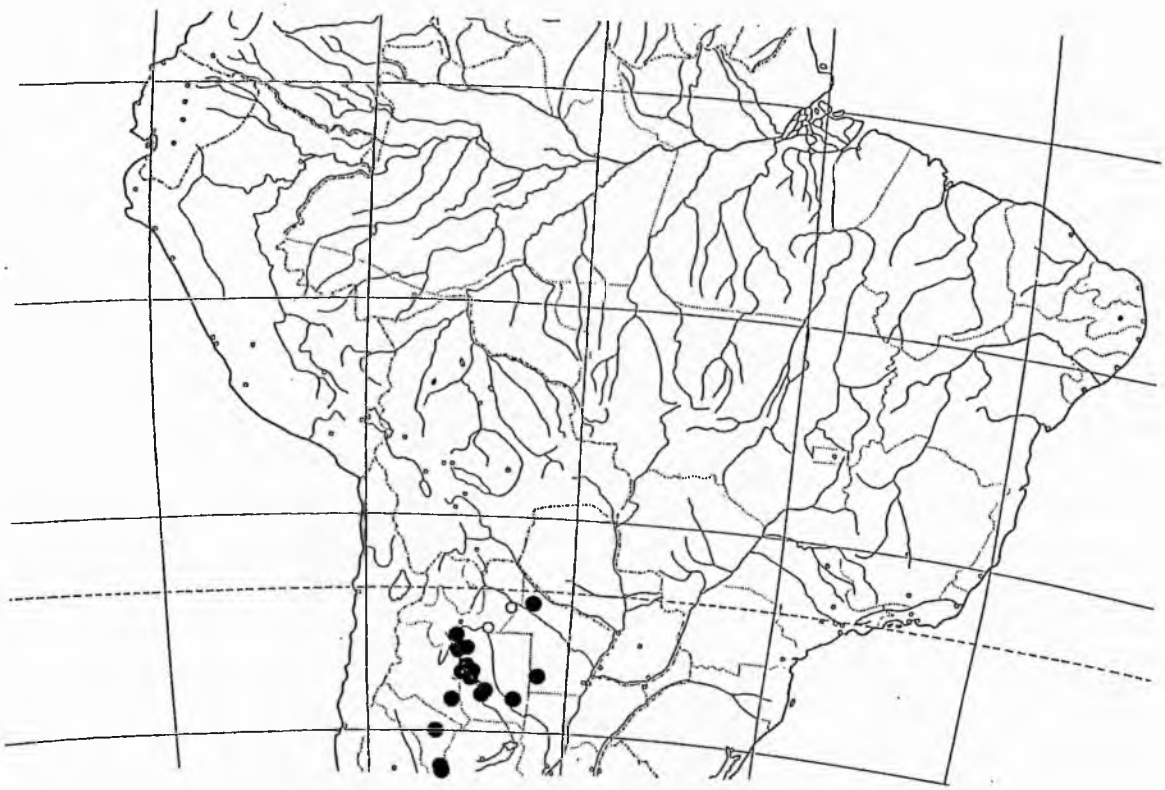
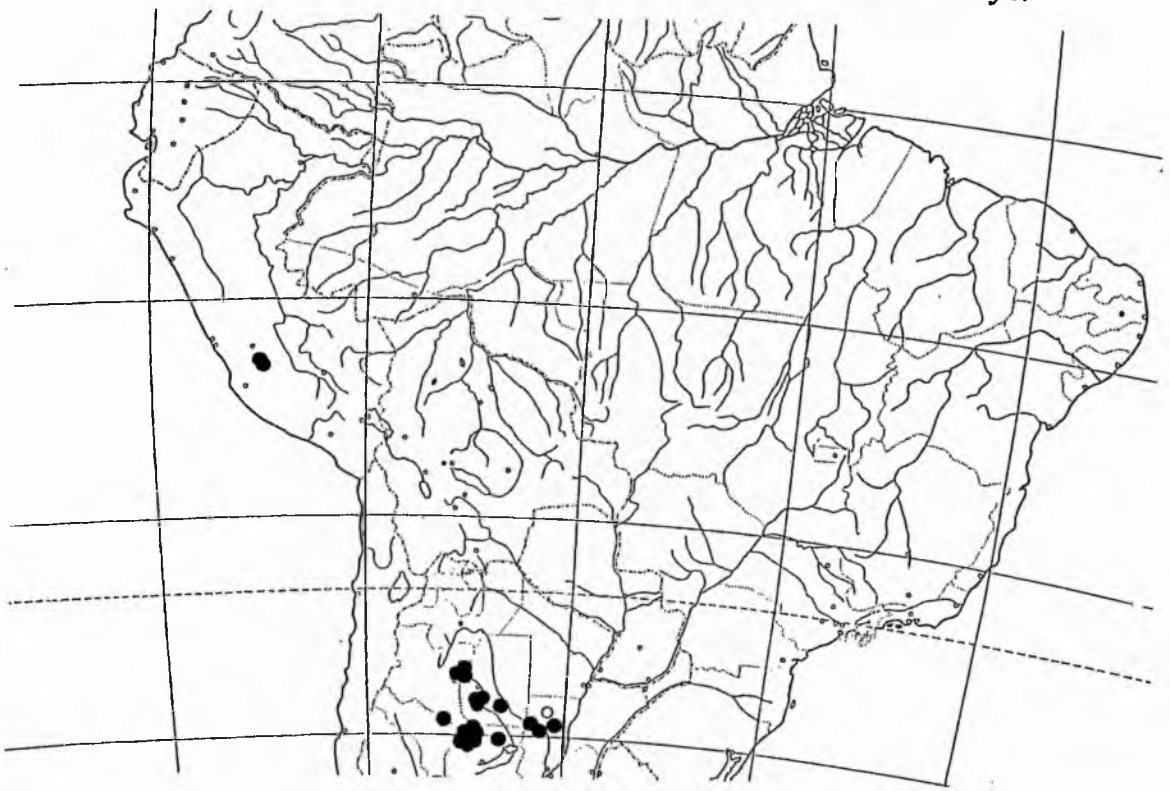


Fig. 5.19: Distribution map of *Prosopis sericantha*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.20: Distribution map of *Prosopis reptans* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



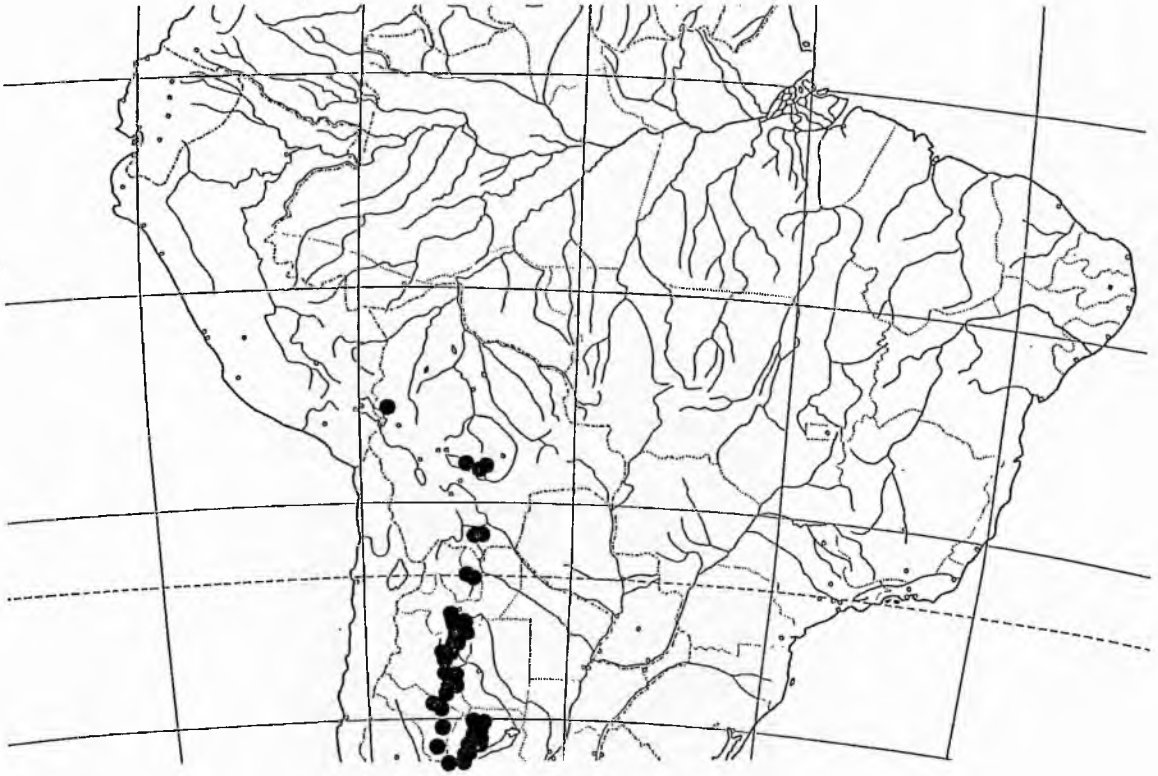
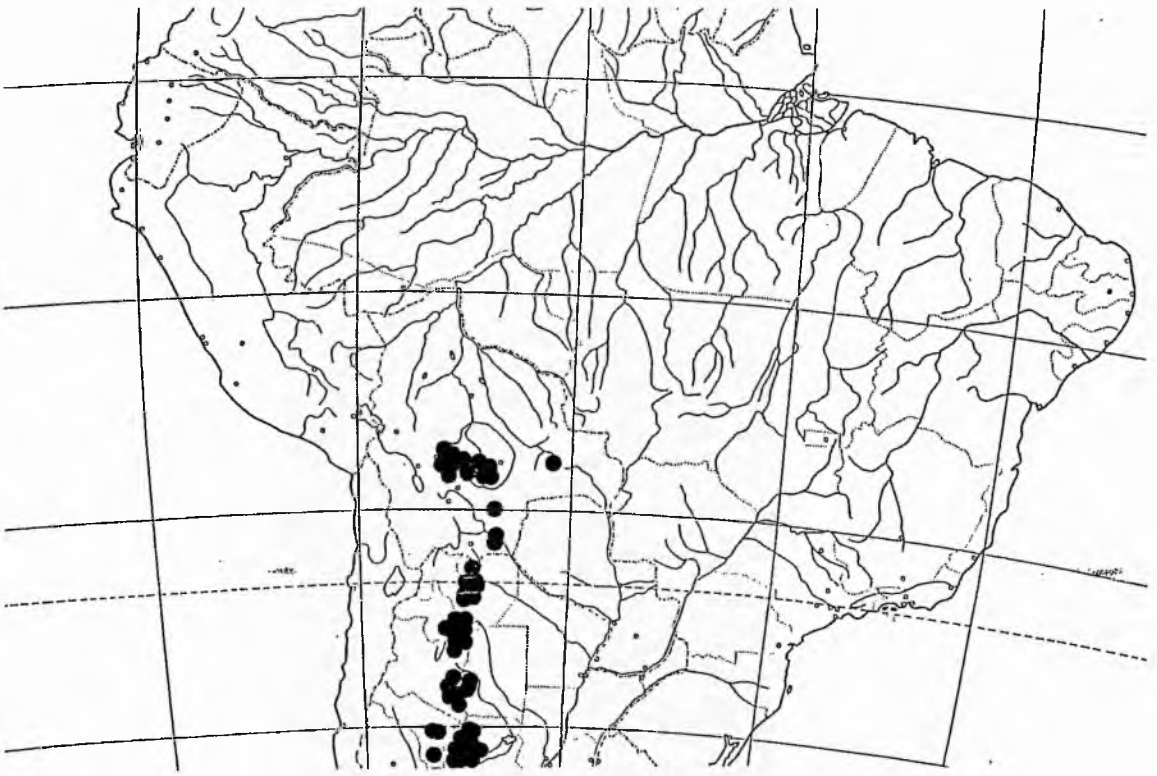


Fig. 5.21: Distribution map of *Lythraea ternifolia*.

Fig. 5.22: Distribution map of *Schinopsis haenkeana*.



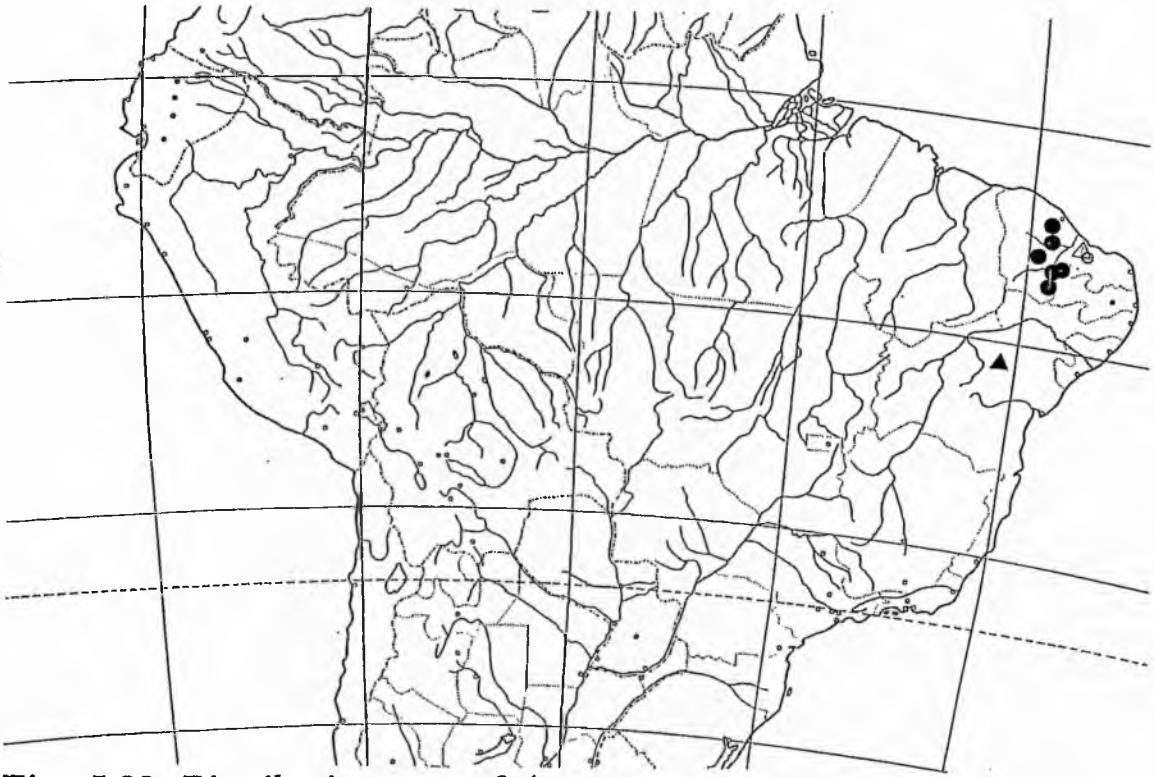
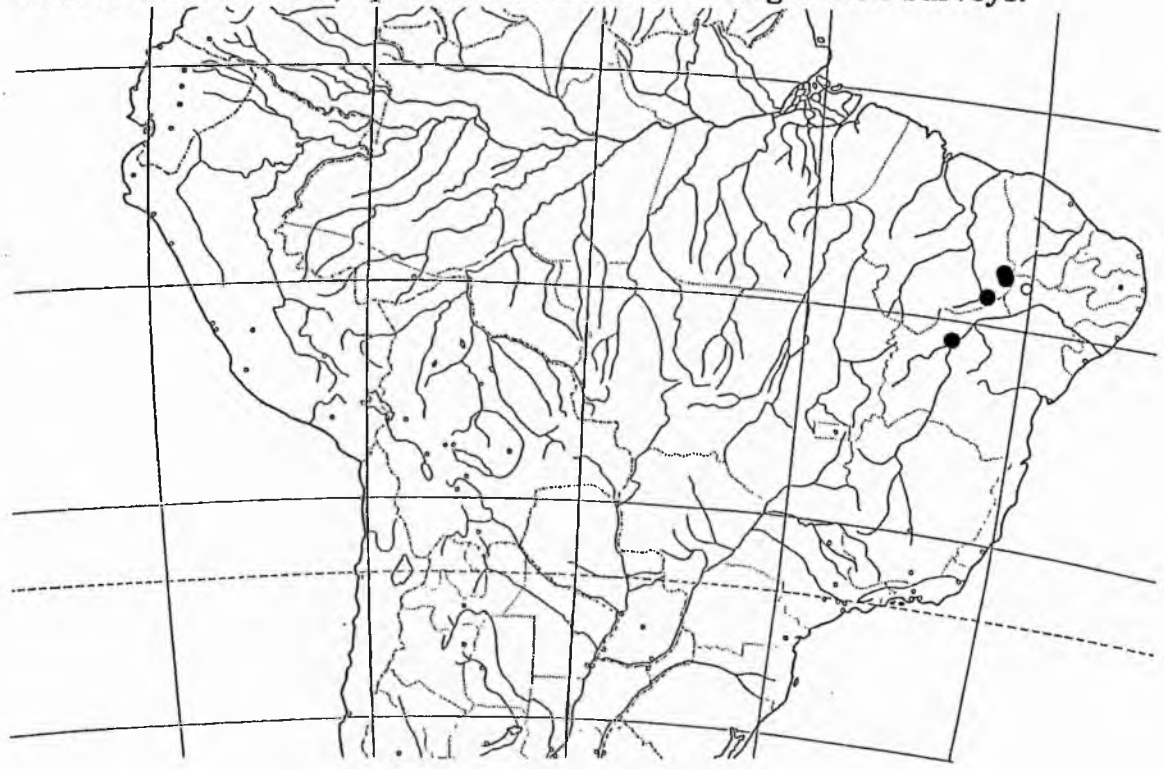


Fig. 5.23: Distribution map of *Auxemma oncocalyx* (circles) and *A. glazioviana* (triangles). Solid black dots/triangles: herbarium exsiccata; open circles/triangles: citations in vegetation surveys.

Fig. 5.24: Distribution map of *Fraunhoffera multiflora*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



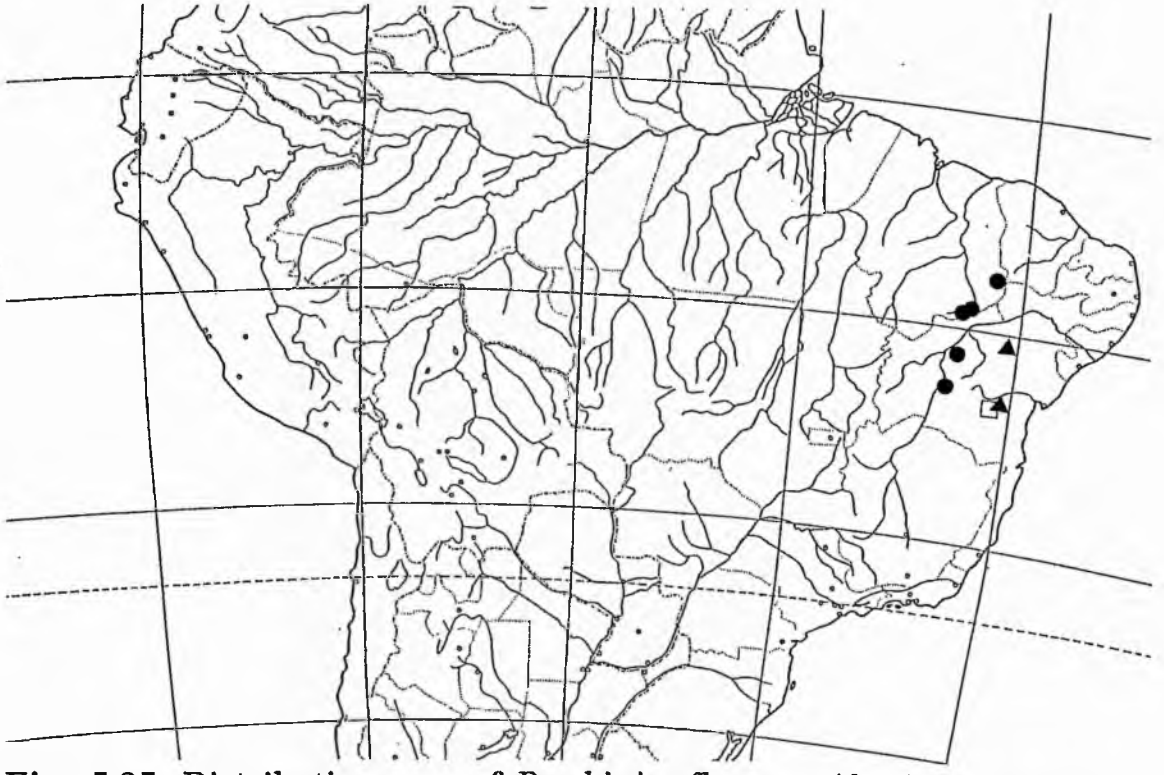
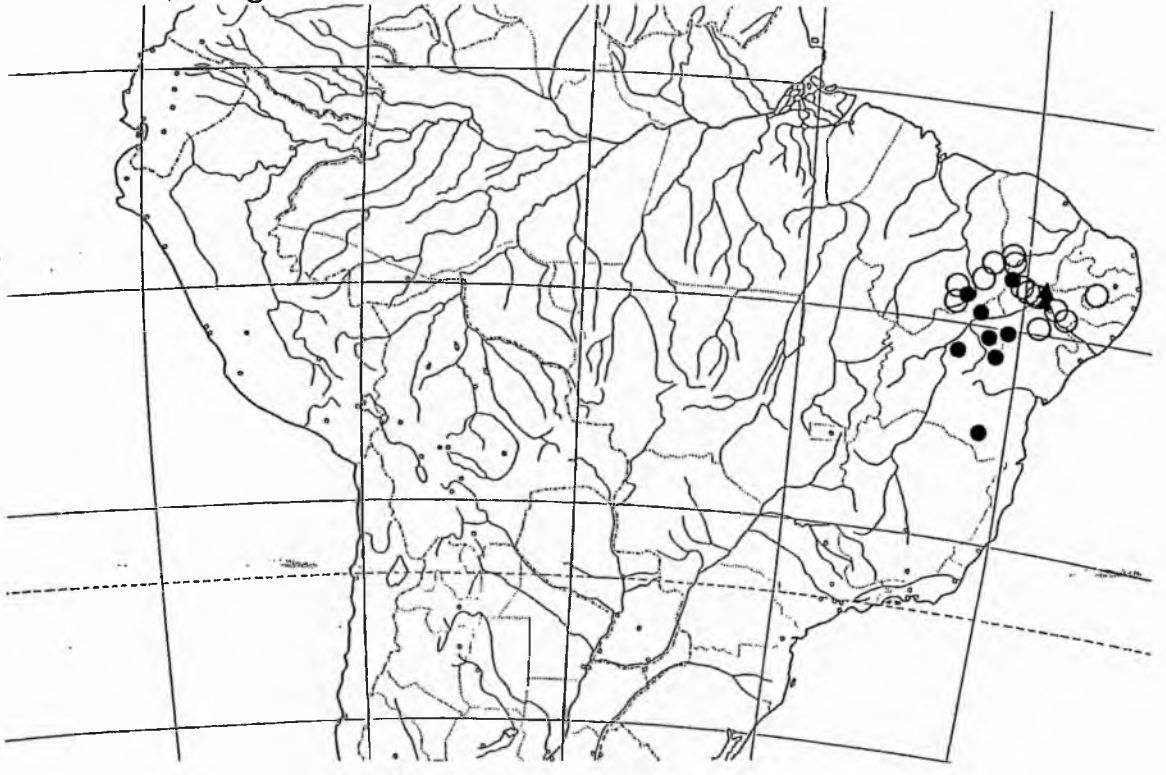


Fig. 5.25: Distribution map of *Bauhinia flexuosa* (dots), *B. estivana* (triangles) and *B. catingae* (open square).

Fig. 5.26: Distribution map of *Cordia leucocephala* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and *C. dardani* (triangles).



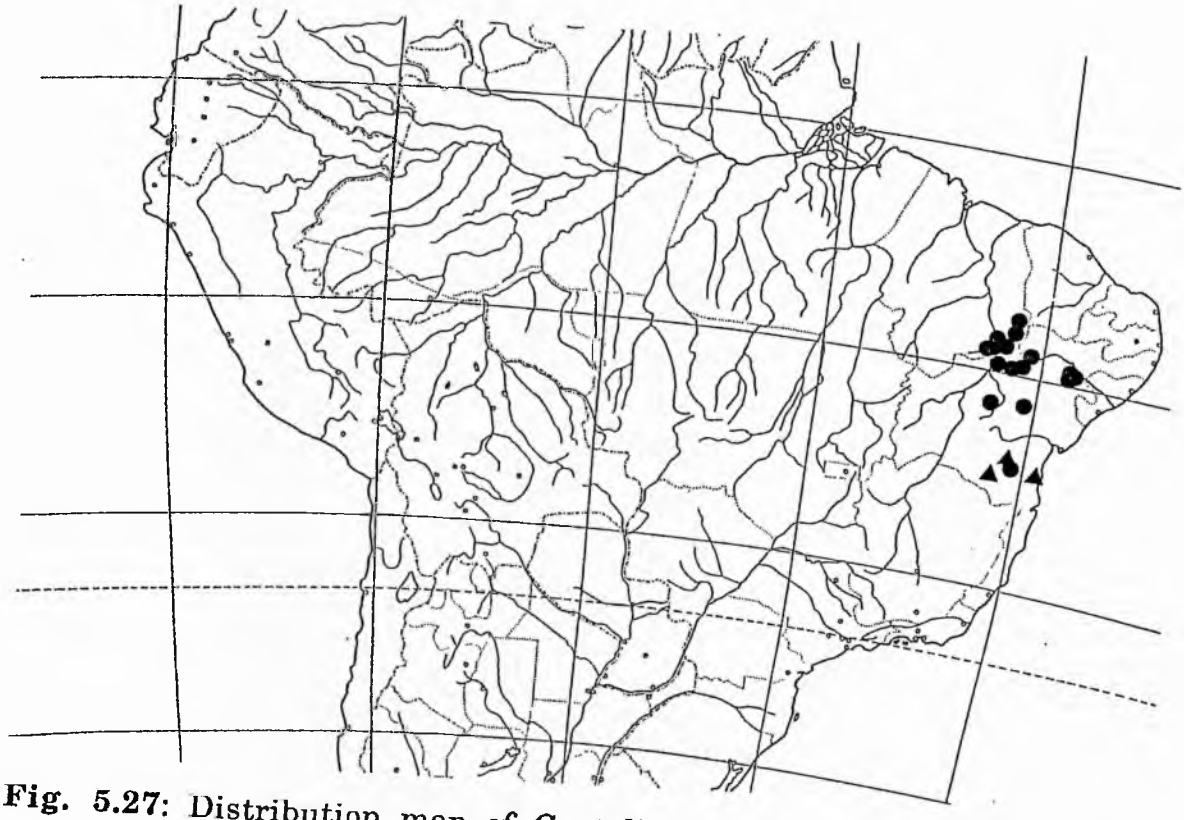
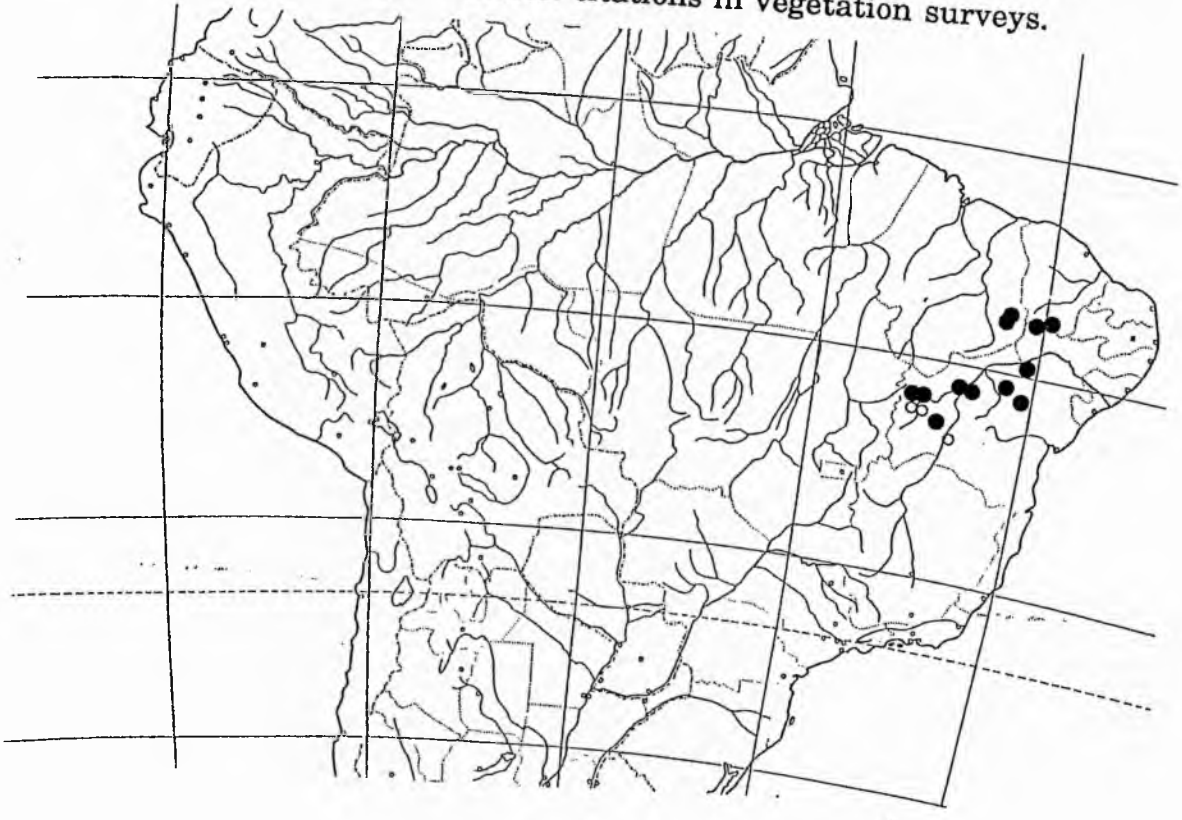


Fig. 5.27: Distribution map of *Cratylia mollis* (dots) and *C. nuda* (triangles).

Fig. 5.28: Distribution map of *Hymenaea eriogyne* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



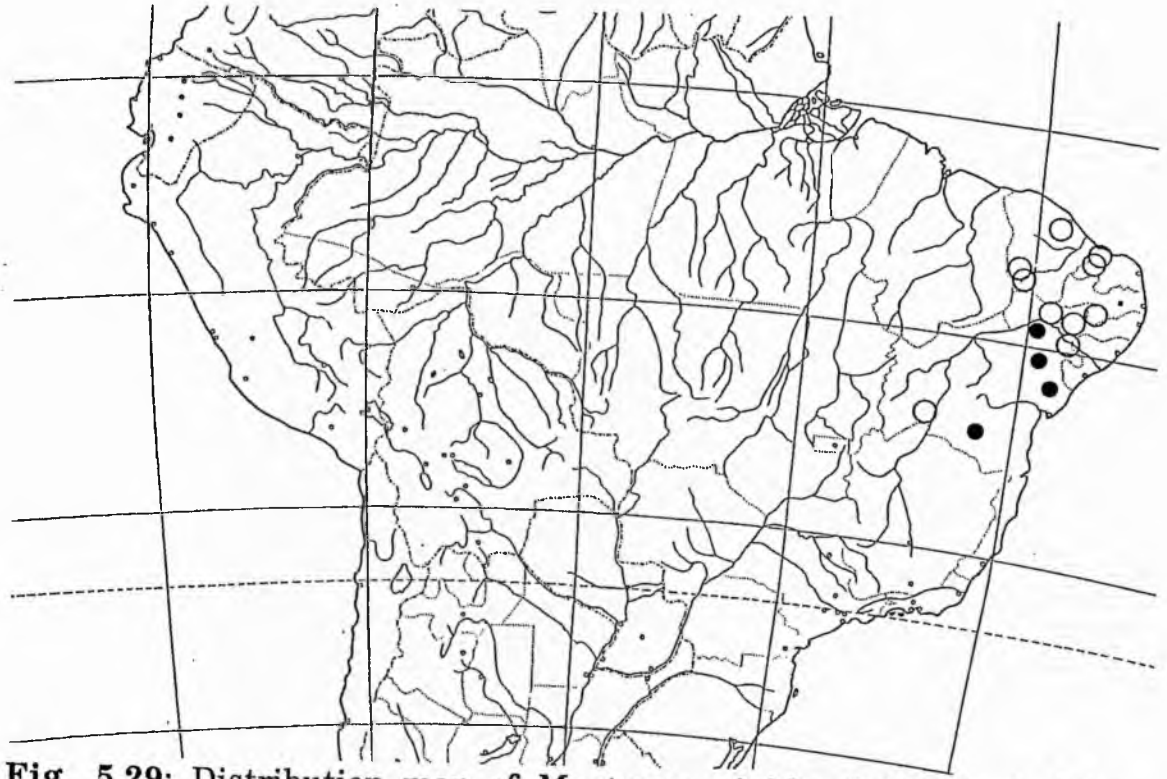
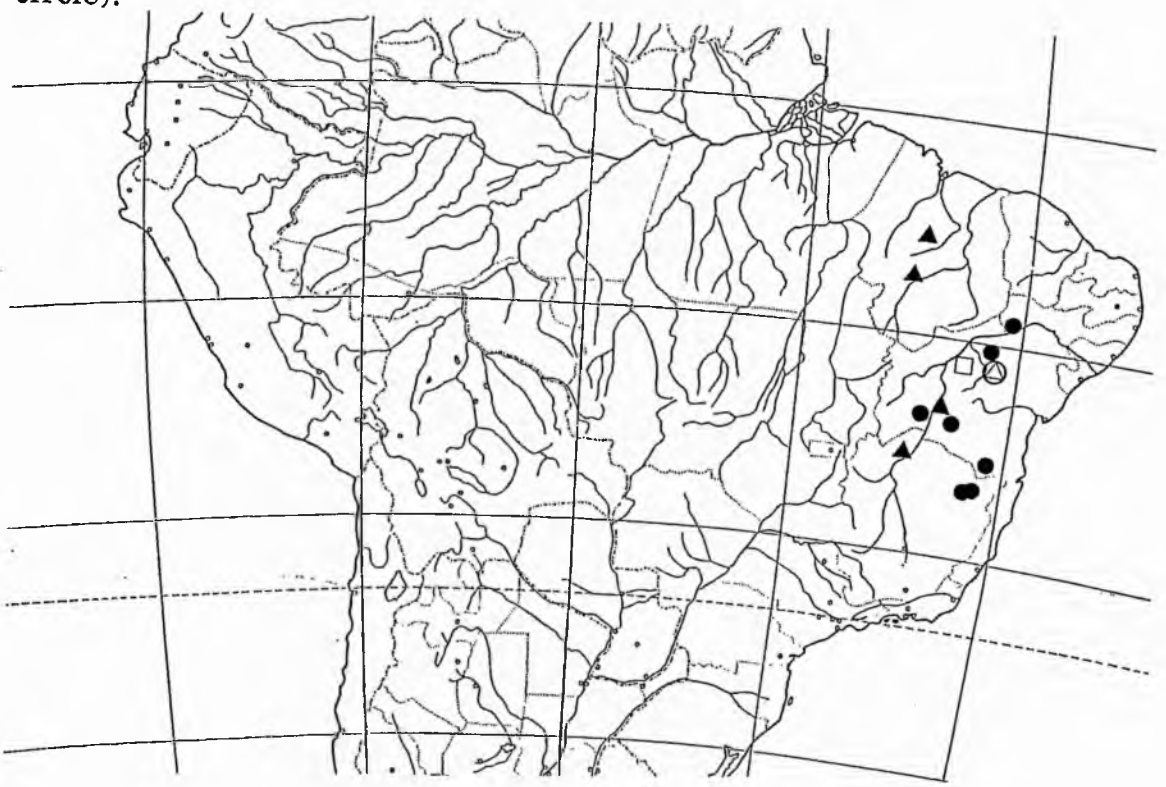


Fig. 5.29: Distribution map of *Maytenus rigida*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.30: Distribution map of *Mimosa adenophylla* (dots), *M. exalbescens* (triangles), *M. glaucula* (open square) and *M. morroënsis* (triangle in circle).



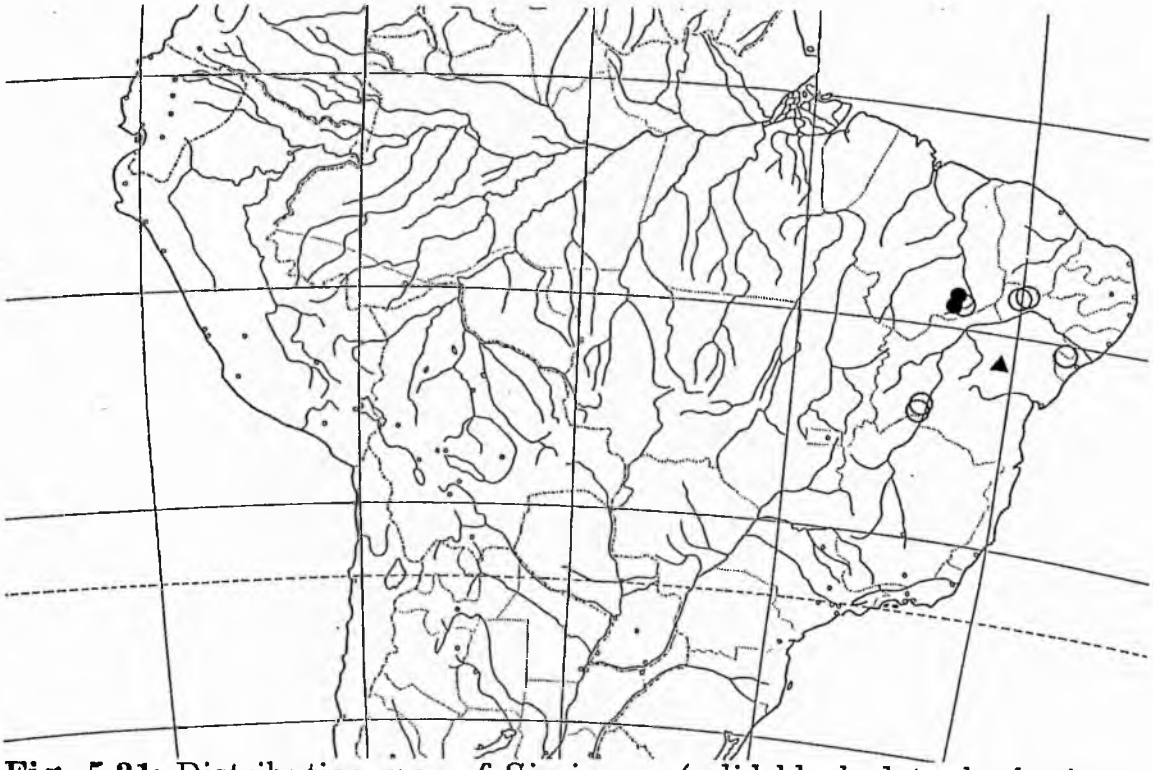
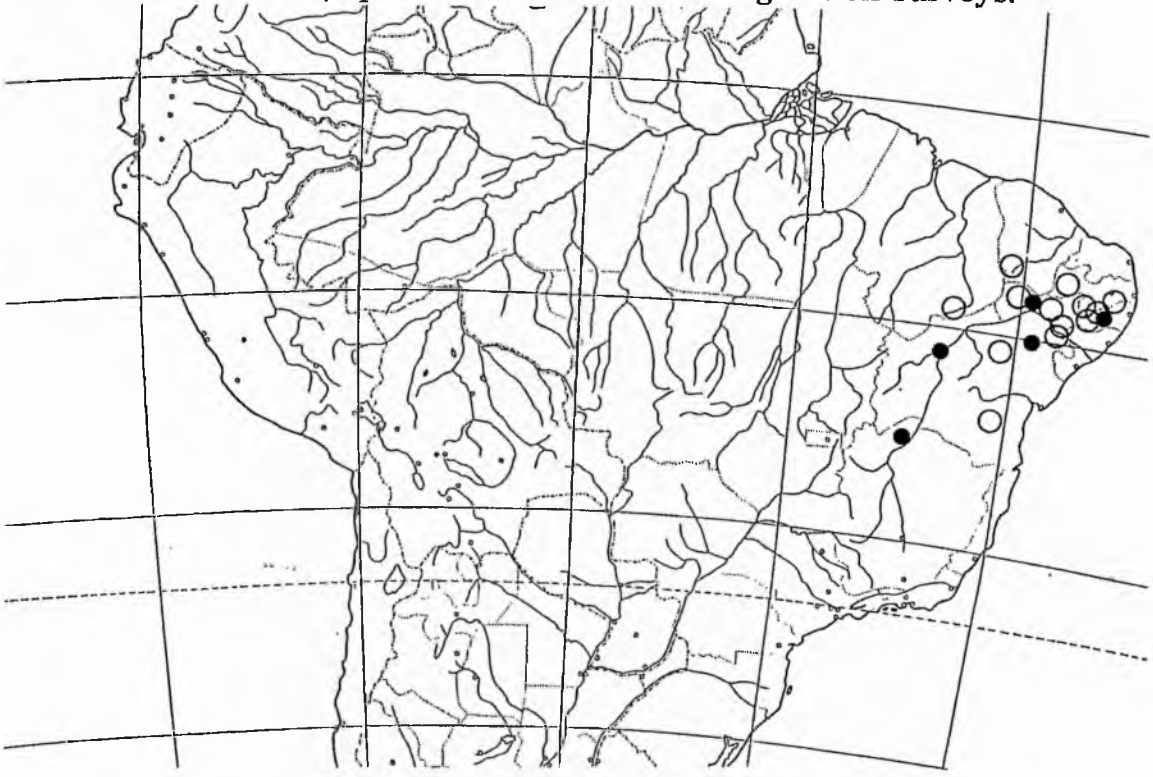


Fig. 5.31: Distribution map of *Simira* sp (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and *Alseis involuta* (triangle).

Fig. 5.32: Distribution map of *Spondias tuberosa*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



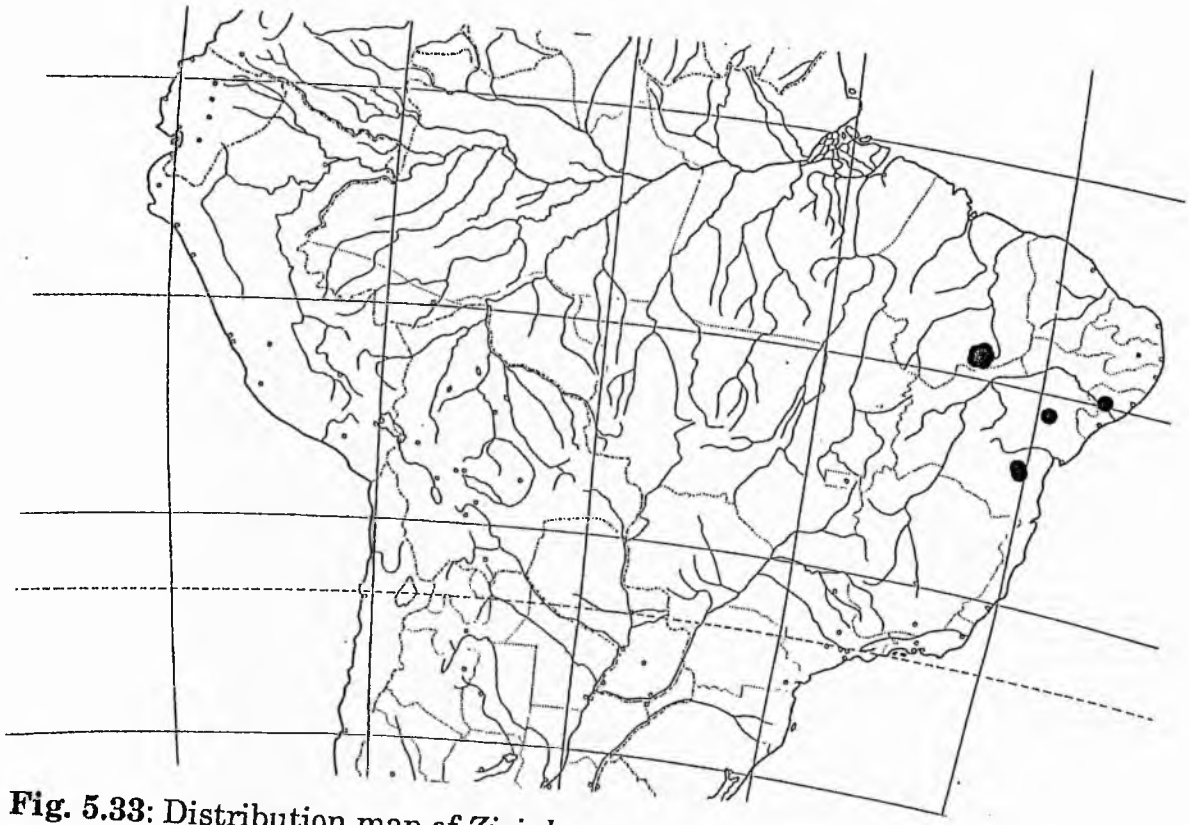
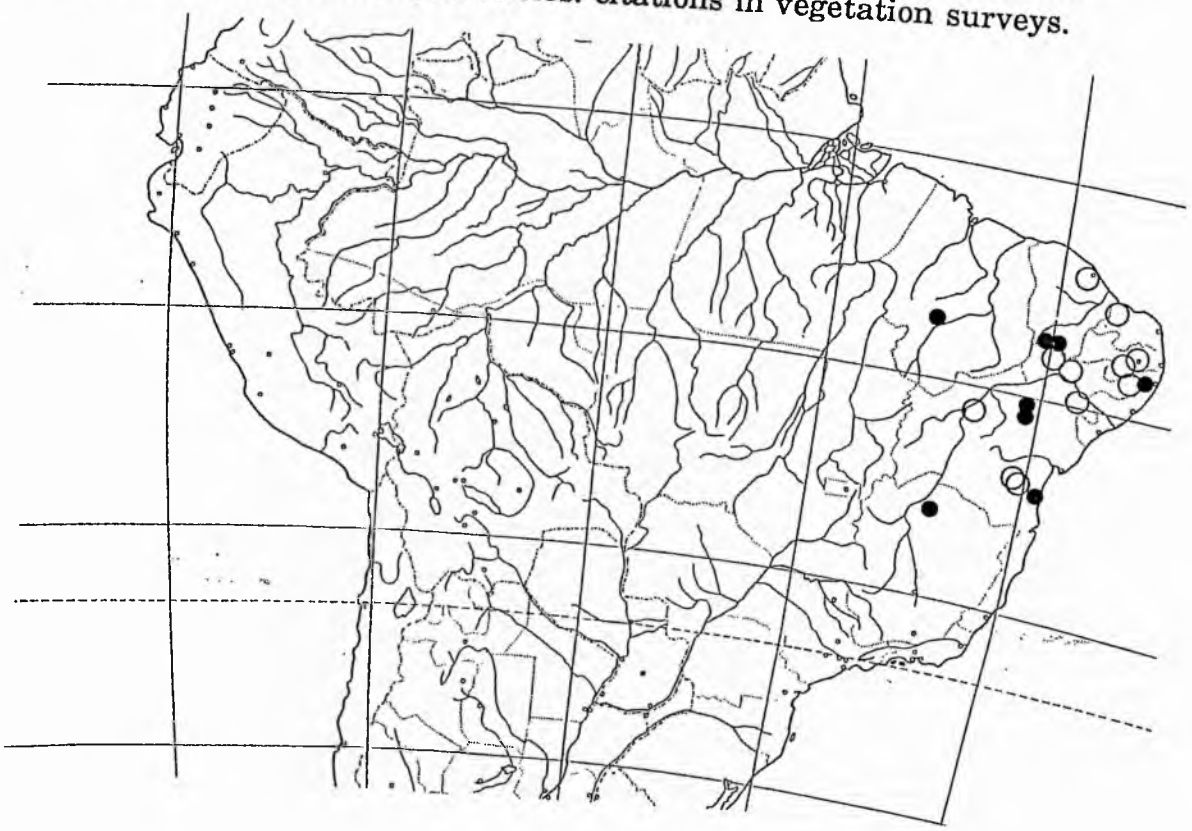


Fig. 5.33: Distribution map of *Ziziphus cotinifolia*.

Fig. 5.34: Distribution map of *Ziziphus joazeiro* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



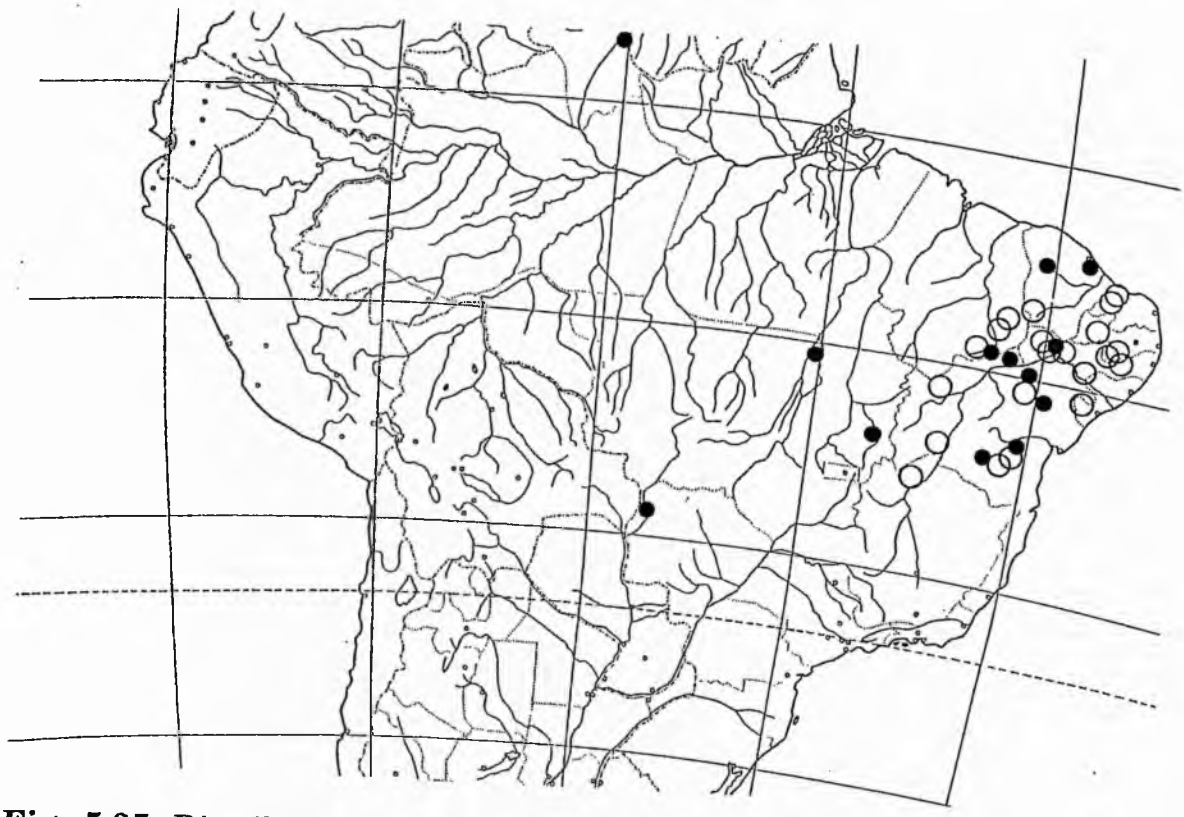
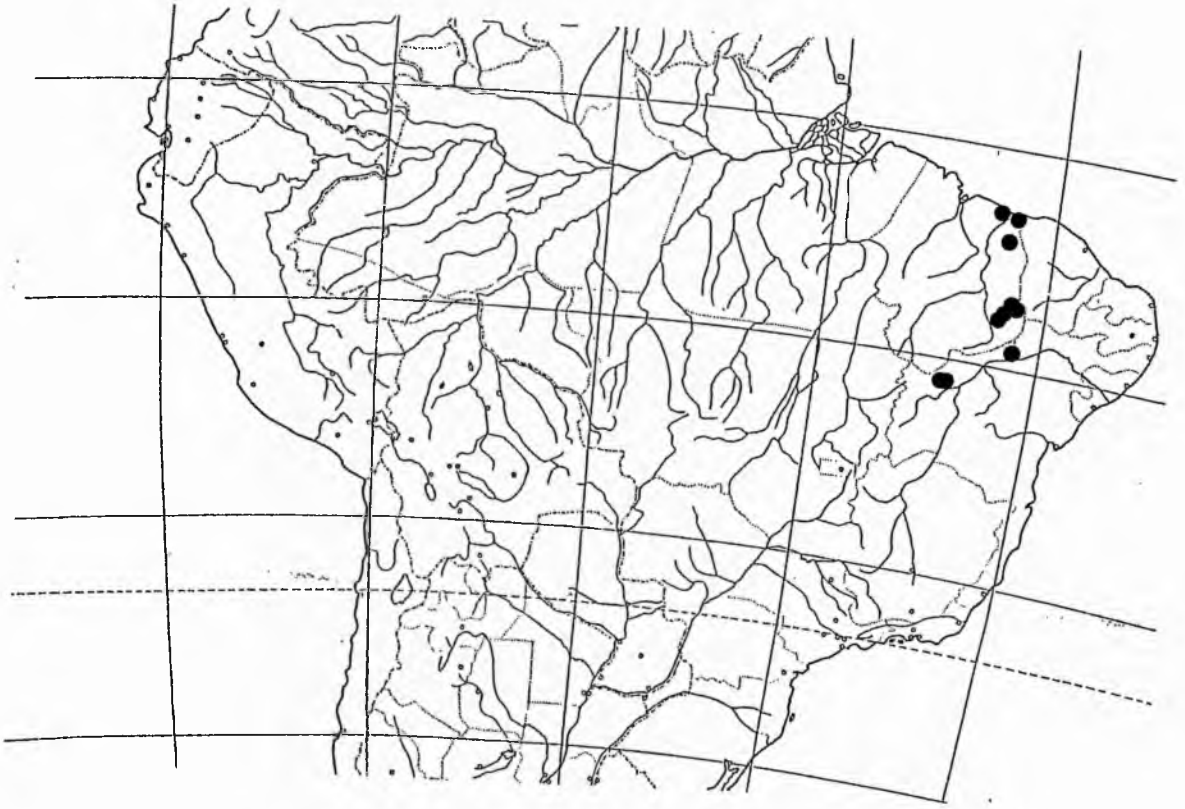


Fig. 5.35: Distribution map of *Commiphora leptophloeos* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.36: Distribution map of *Hymenaea velutina*.



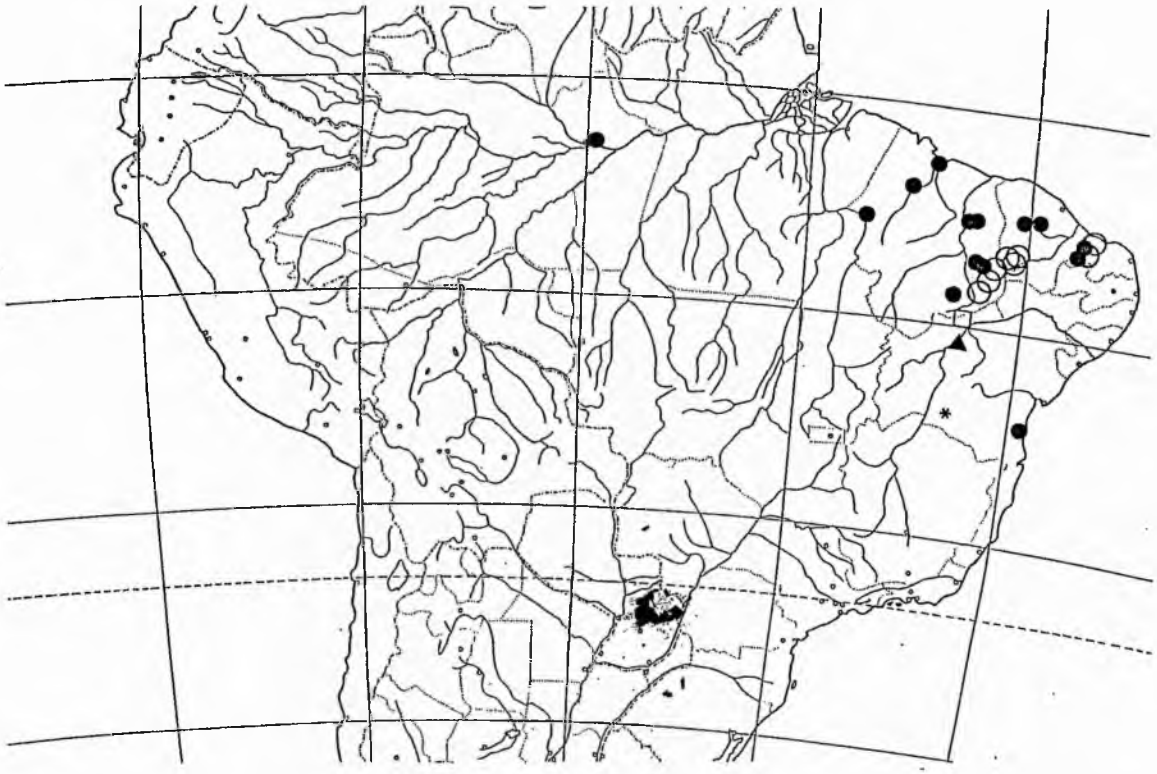


Fig. 5.37: Distribution map of *Mimosa caesalpiniifolia* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys), *M. nothopteris* (open square), *M. xique-xiquensis* (triangle) and *M. coruscaesia* (asterisk).

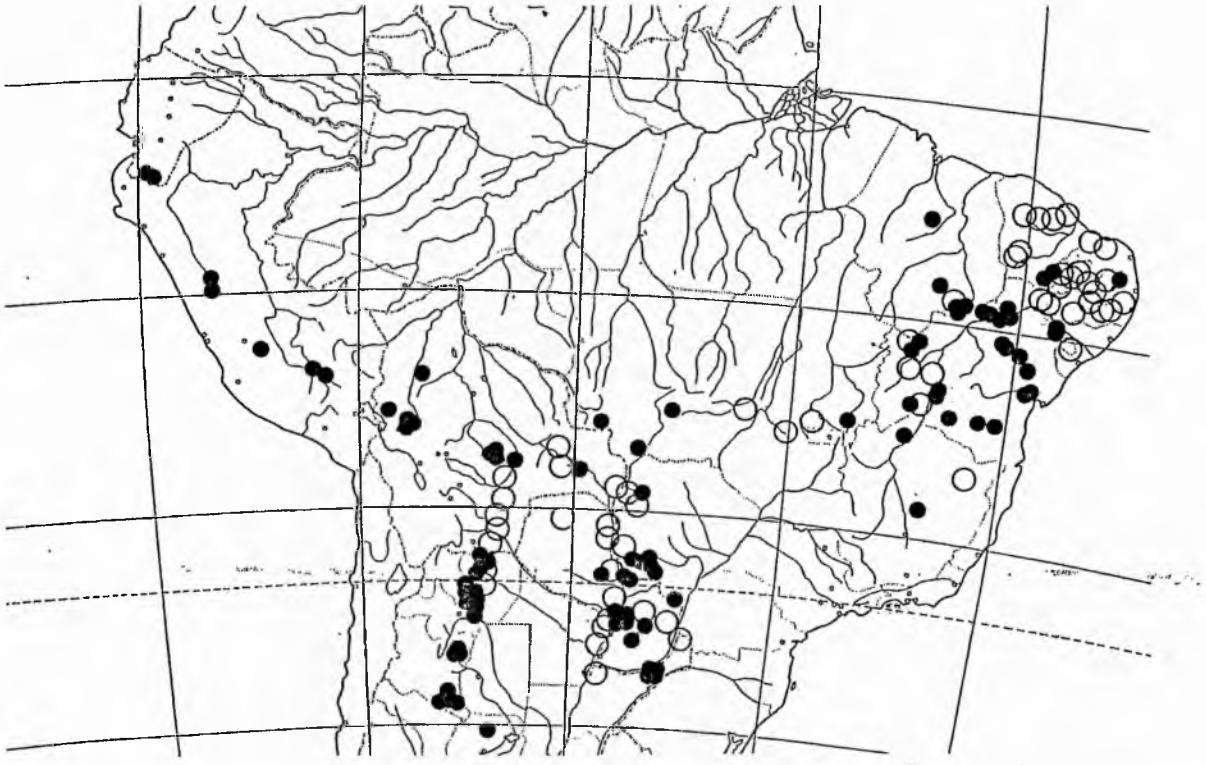


Fig. 5.38: Distribution map of *Anadenanthera colubrina* var. *cebil* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

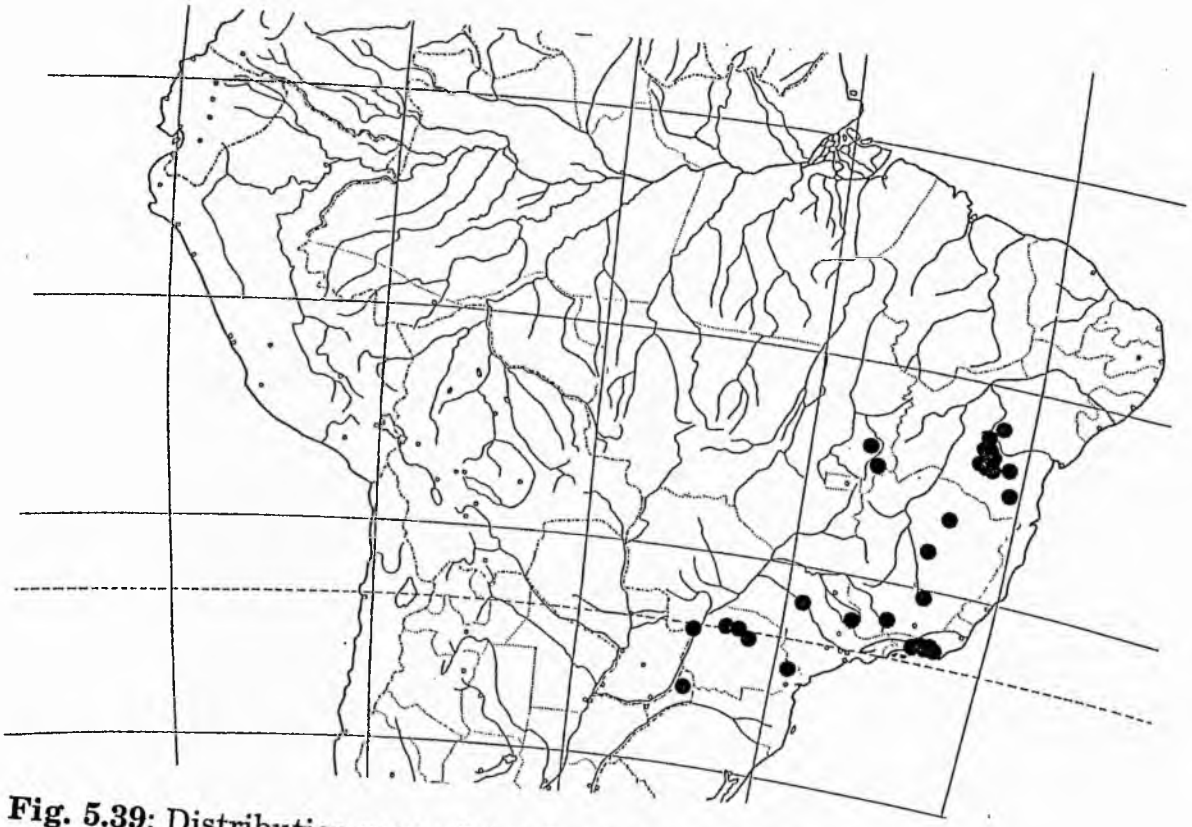
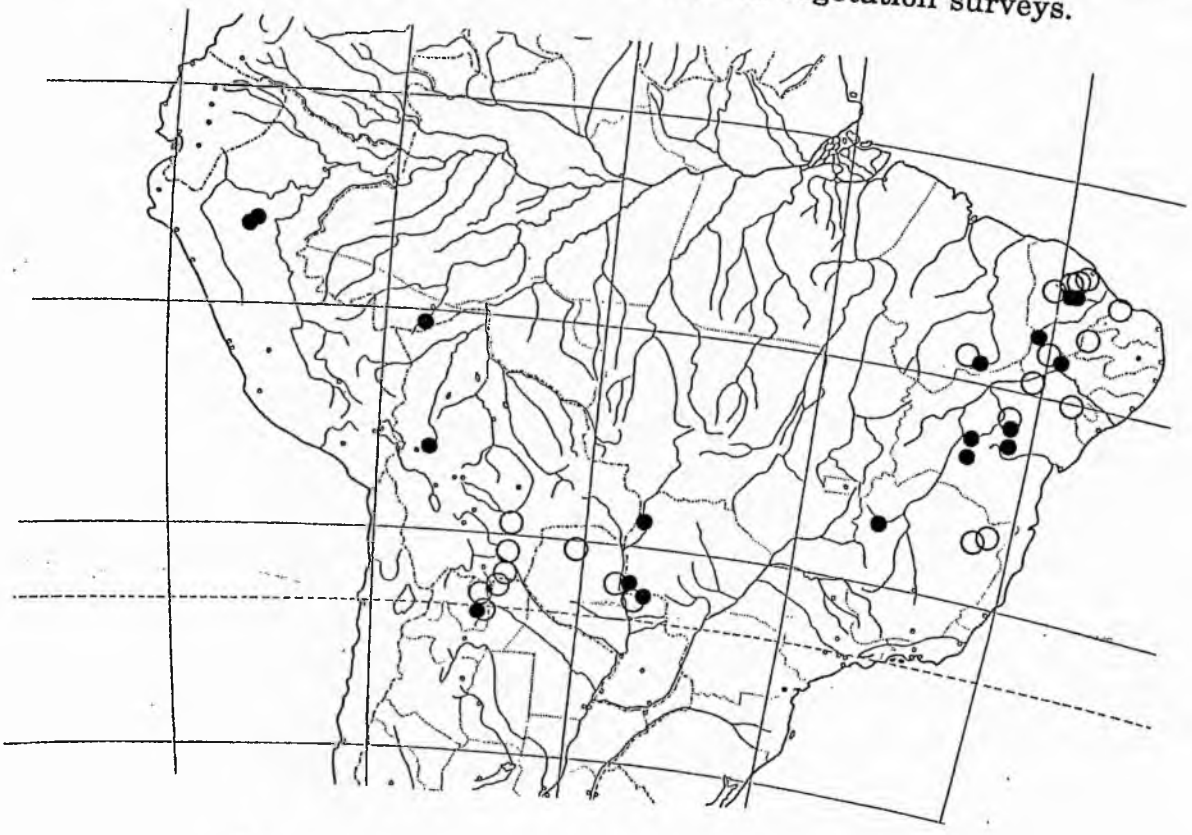


Fig. 5.39: Distribution map of *Anadenanthera colubrina* var. *colubrina*.

Fig. 5.40: Distribution map of *Amburana cearensis* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



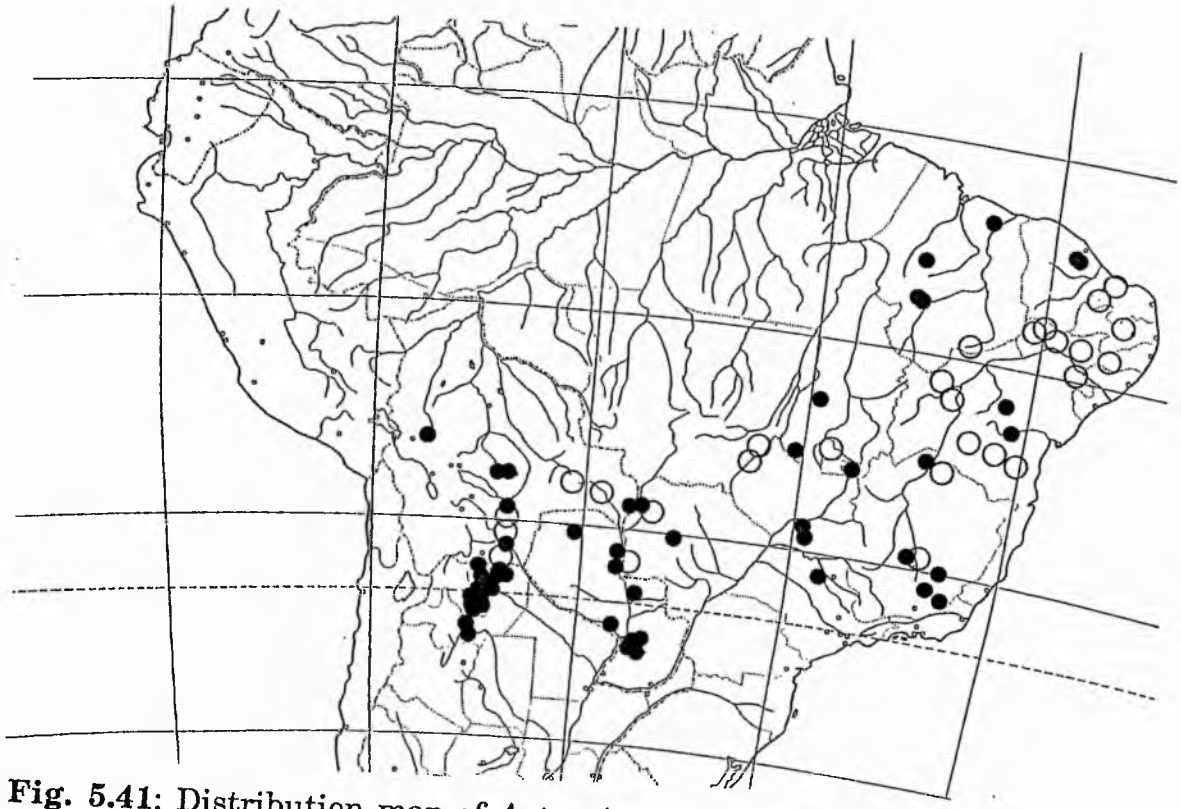
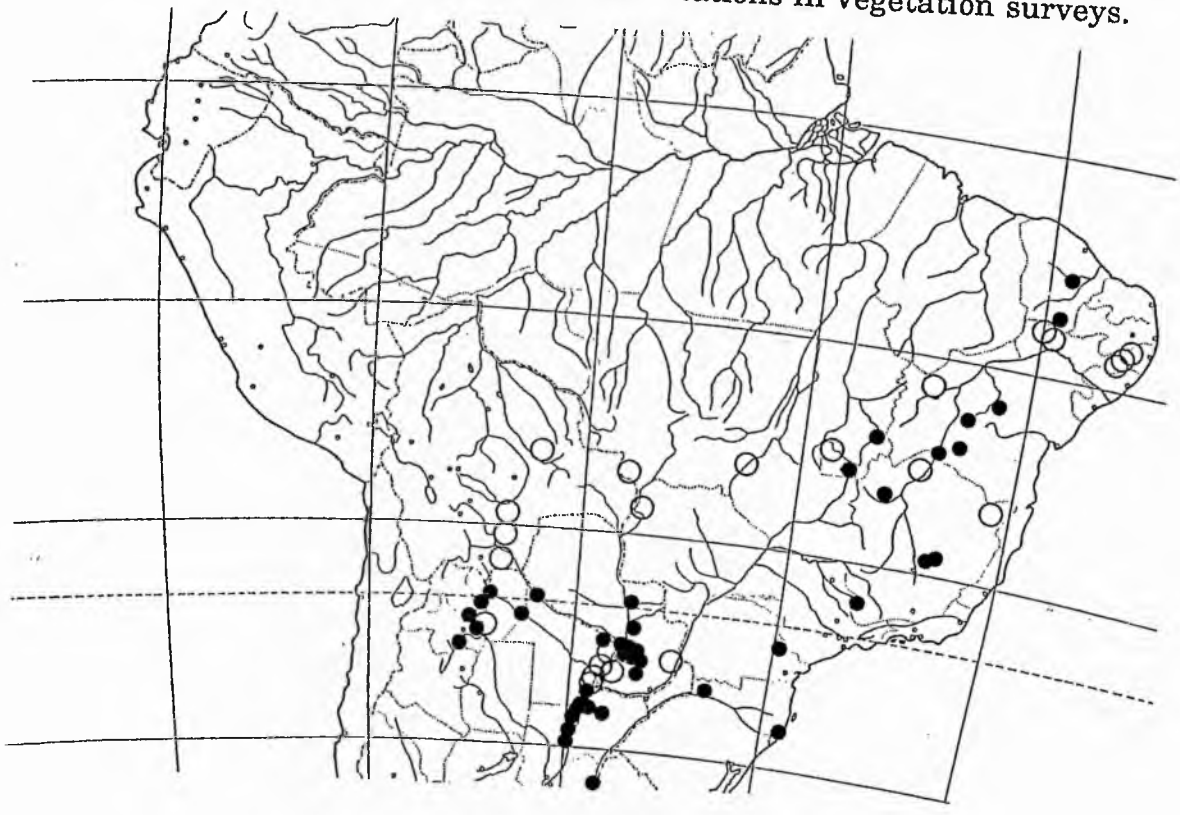


Fig. 5.41: Distribution map of *Astronium urundeuva*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.42: Distribution map of *Enterolobium contortisiliquum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



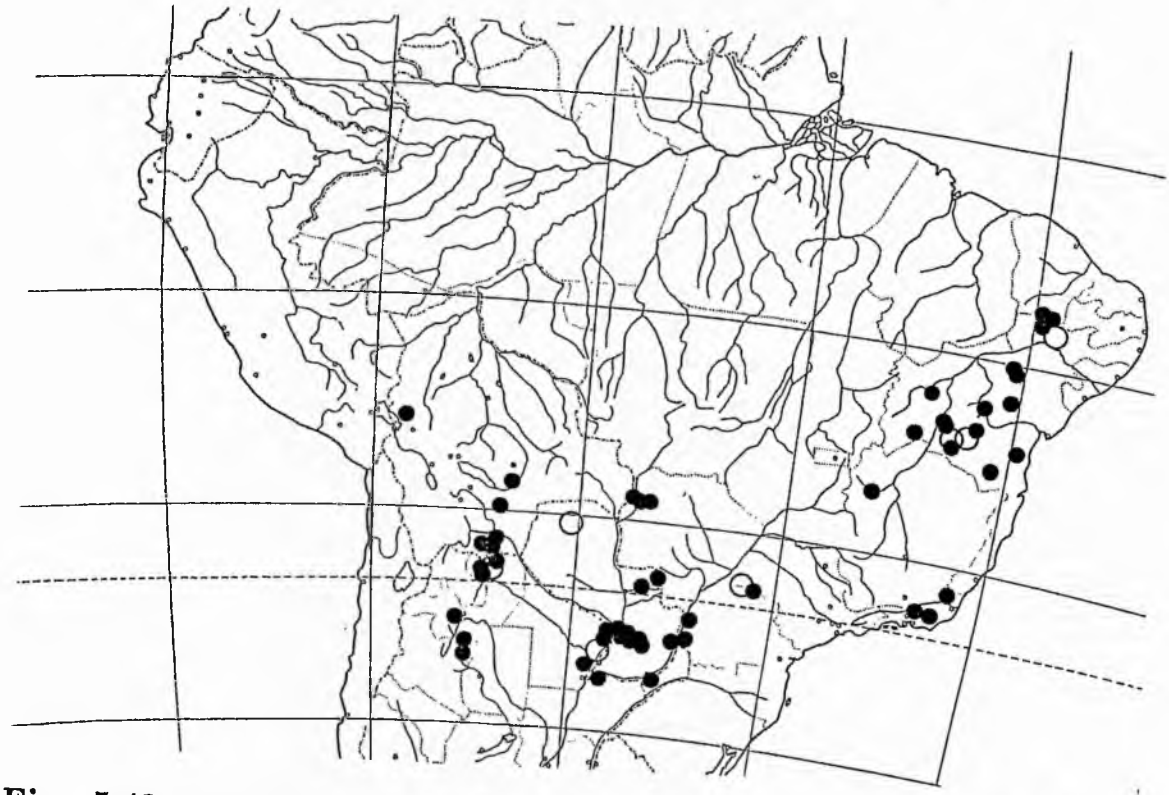
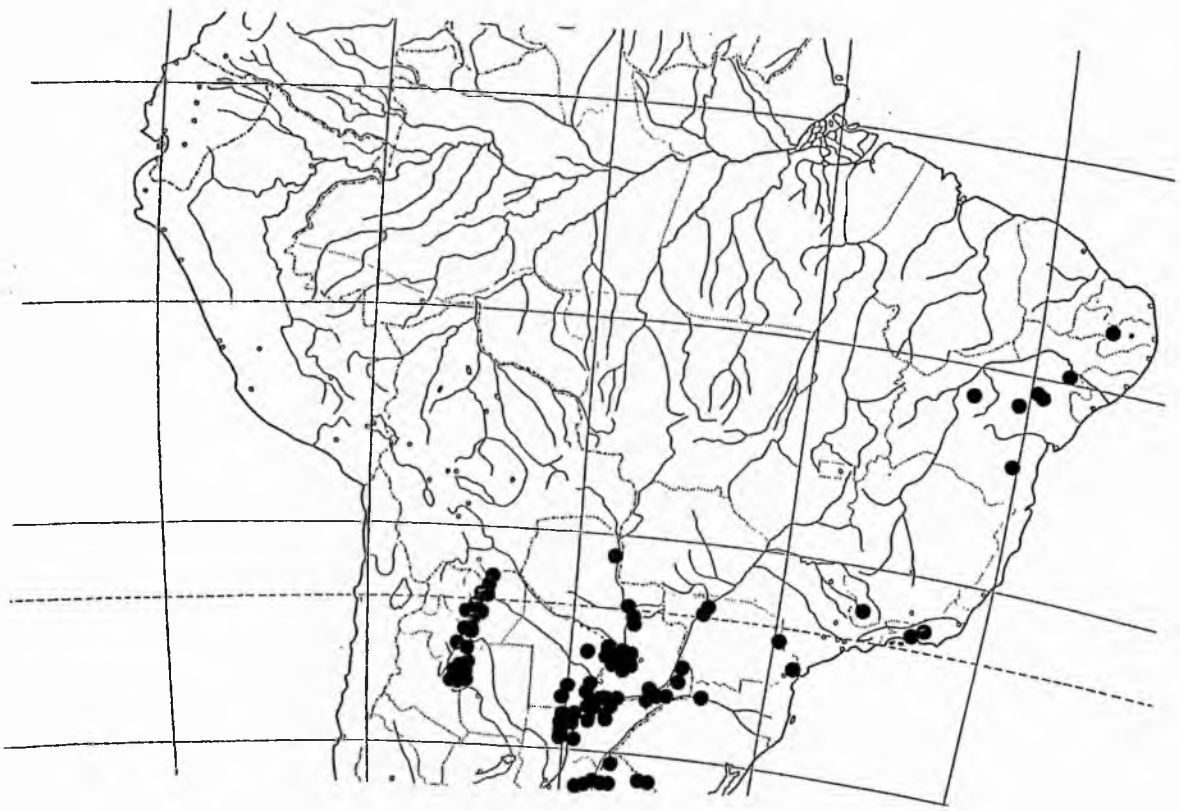


Fig. 5.43: Distribution map of *Pterogyne nitens* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.44: Distribution map of *Ruprechtia laxiflora*.



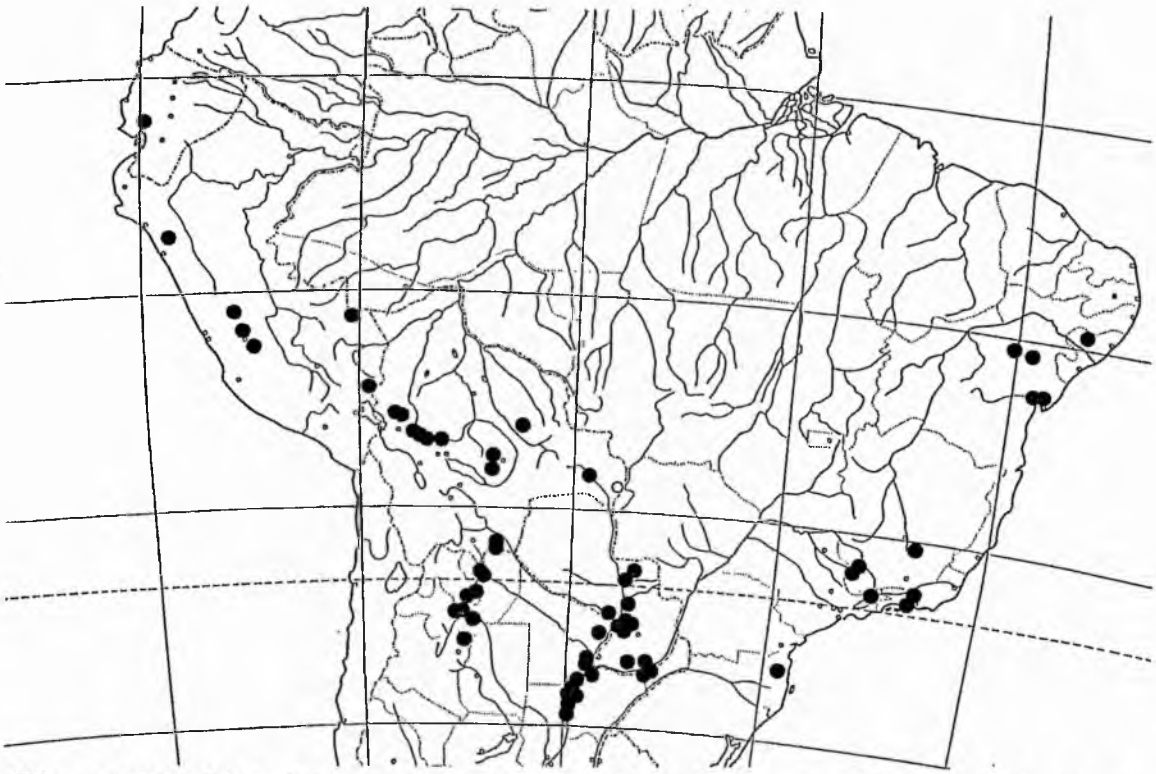
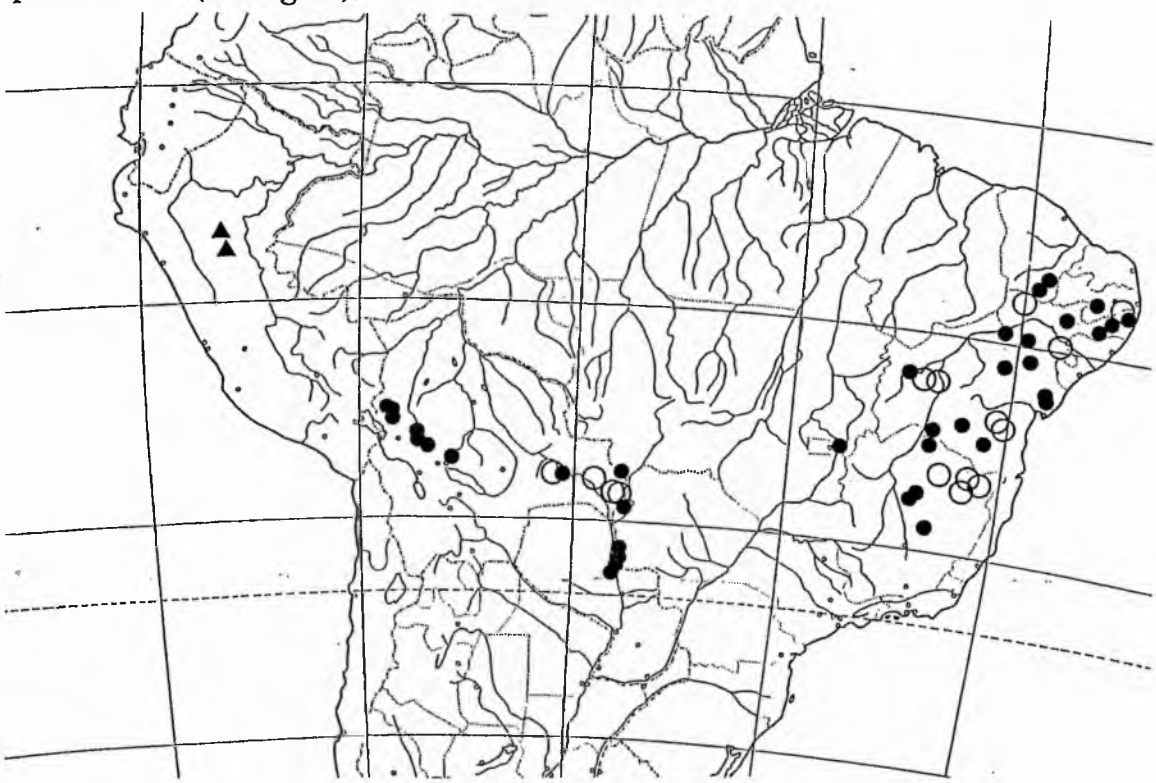


Fig. 5.45: Distribution map of *Celtis pubescens* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.46: Distribution map of *Schinopsis brasiliensis* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and *S. peruviana* (triangles).



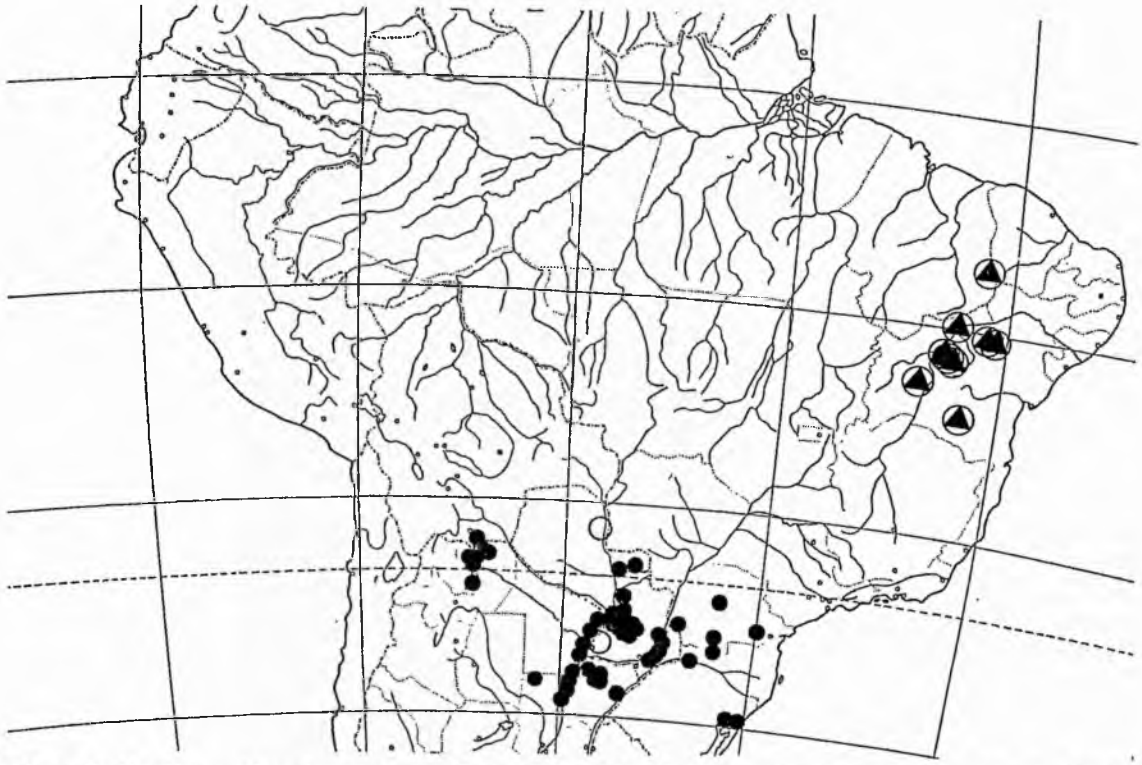
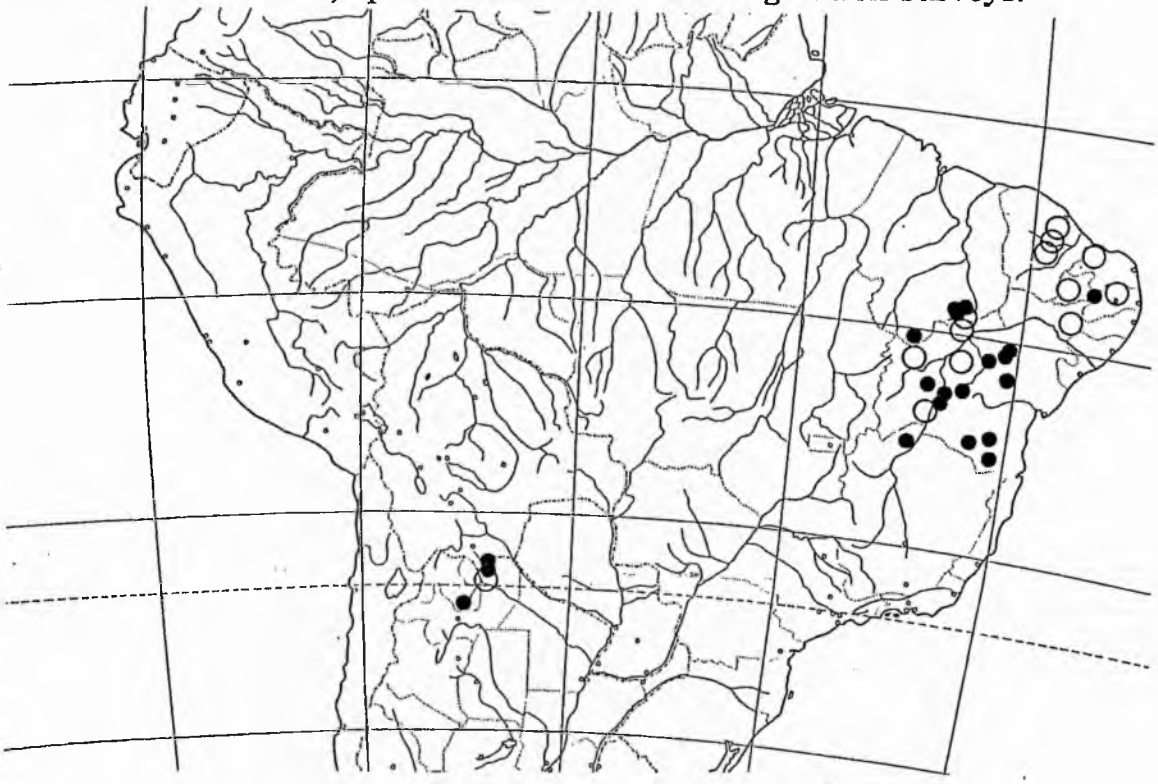


Fig. 5.47: Distribution map of *Patagonula bahiensis* (triangles in circles) and *P. americana* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys).

Fig. 5.48: Distribution map of *Piptadenia viridiflora*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



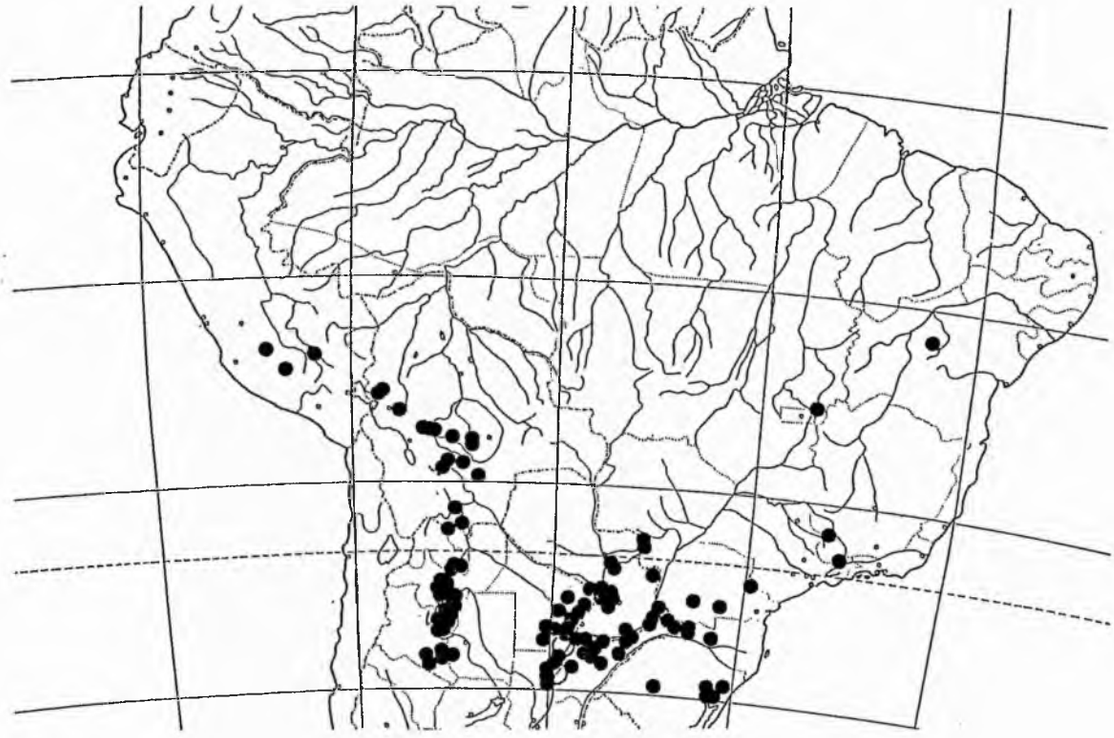
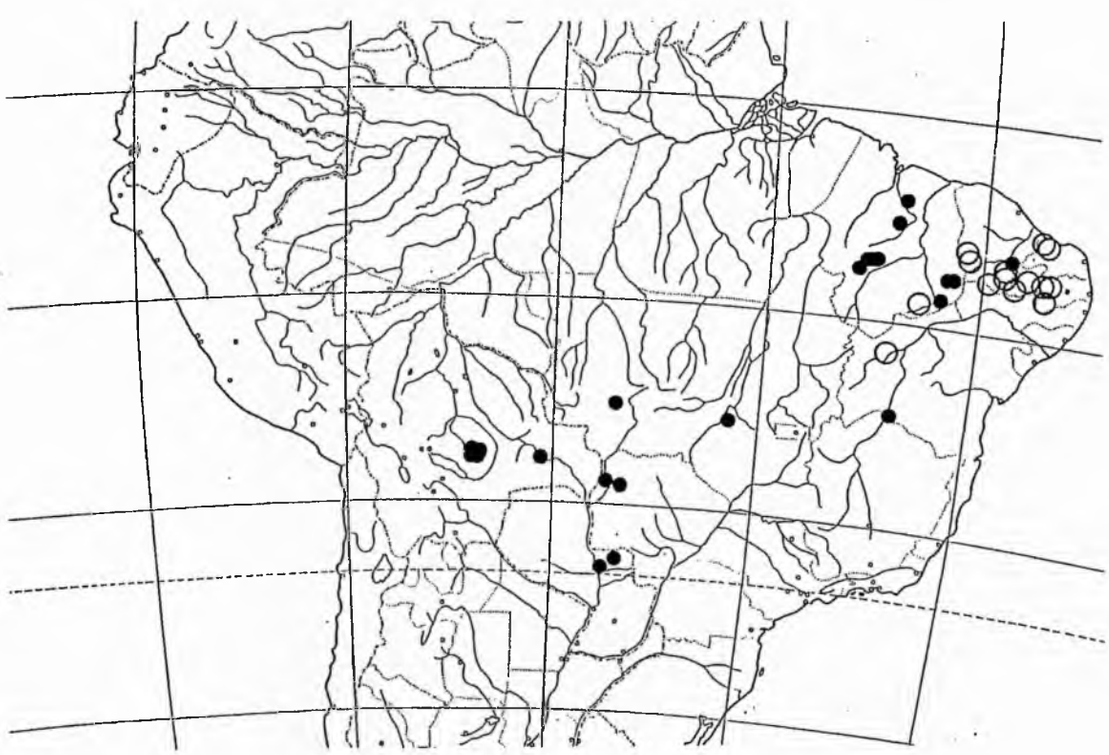


Fig. 5.49: Distribution map of *Carica quercifolia*.

Fig. 5.50: Distribution map of *Combretum leprosum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



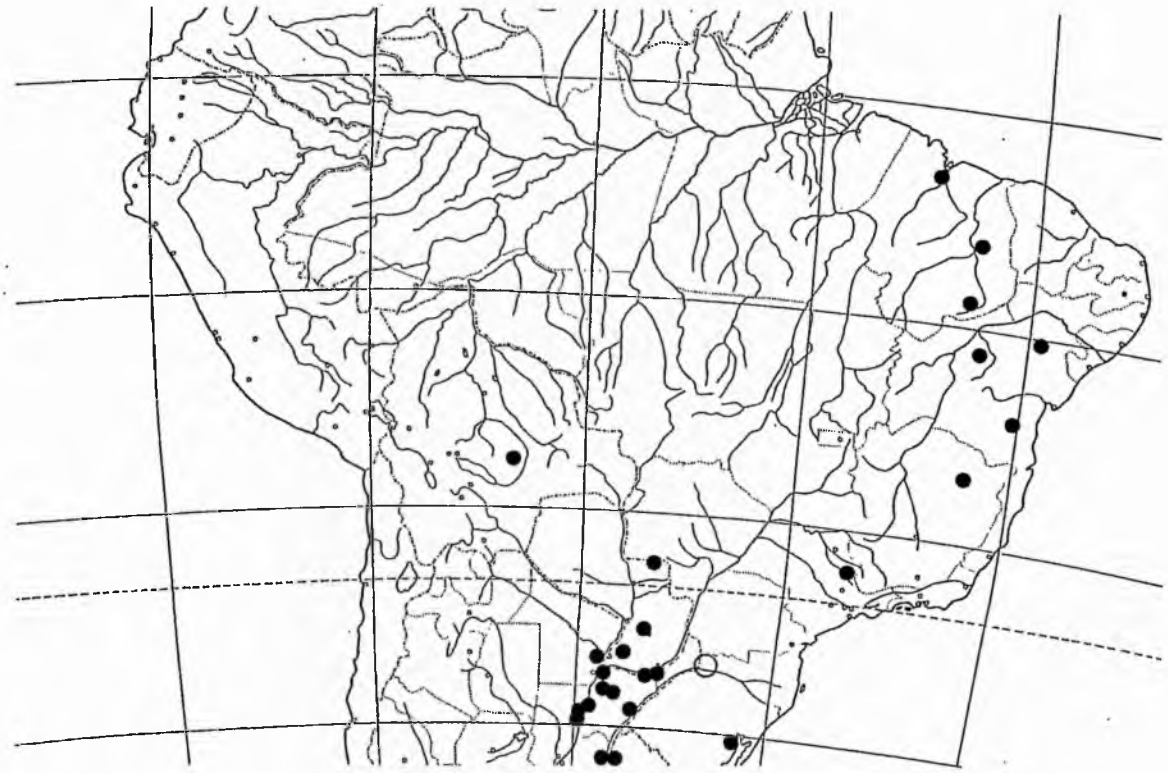
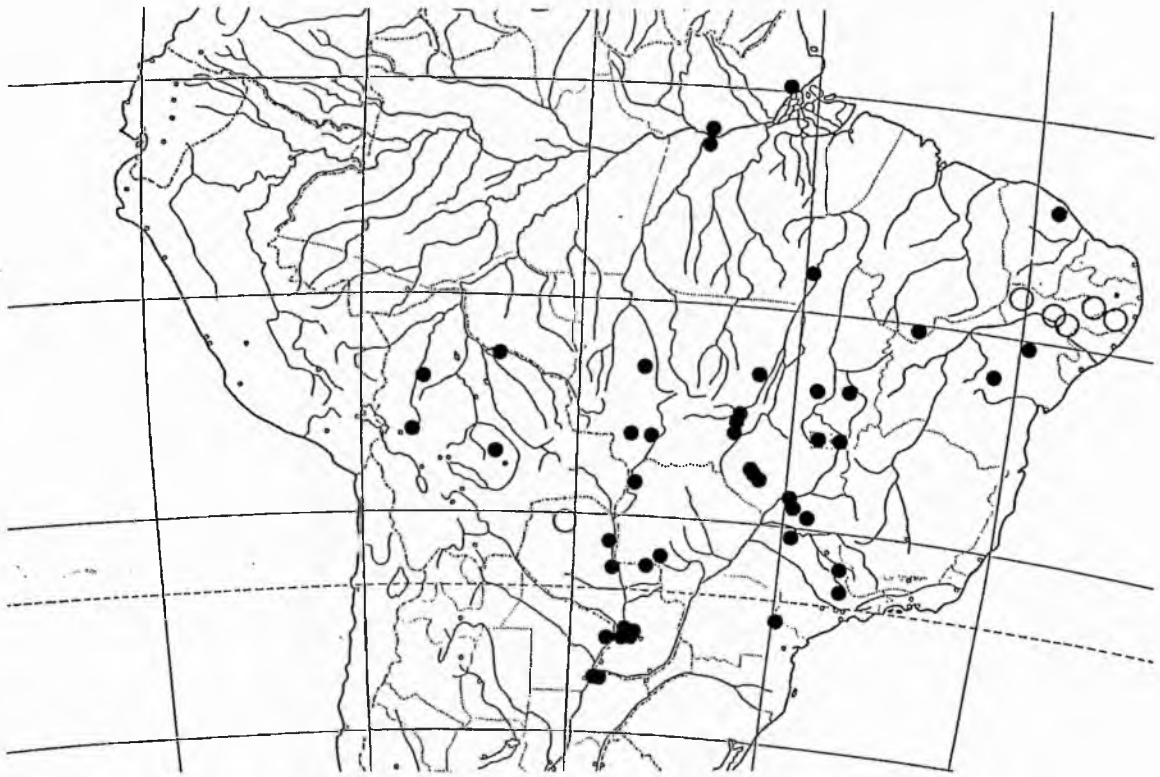


Fig. 5.51: Distribution map of *Pouteria gardneriana*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.52: Distribution map of *Tabebuia caraiba*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



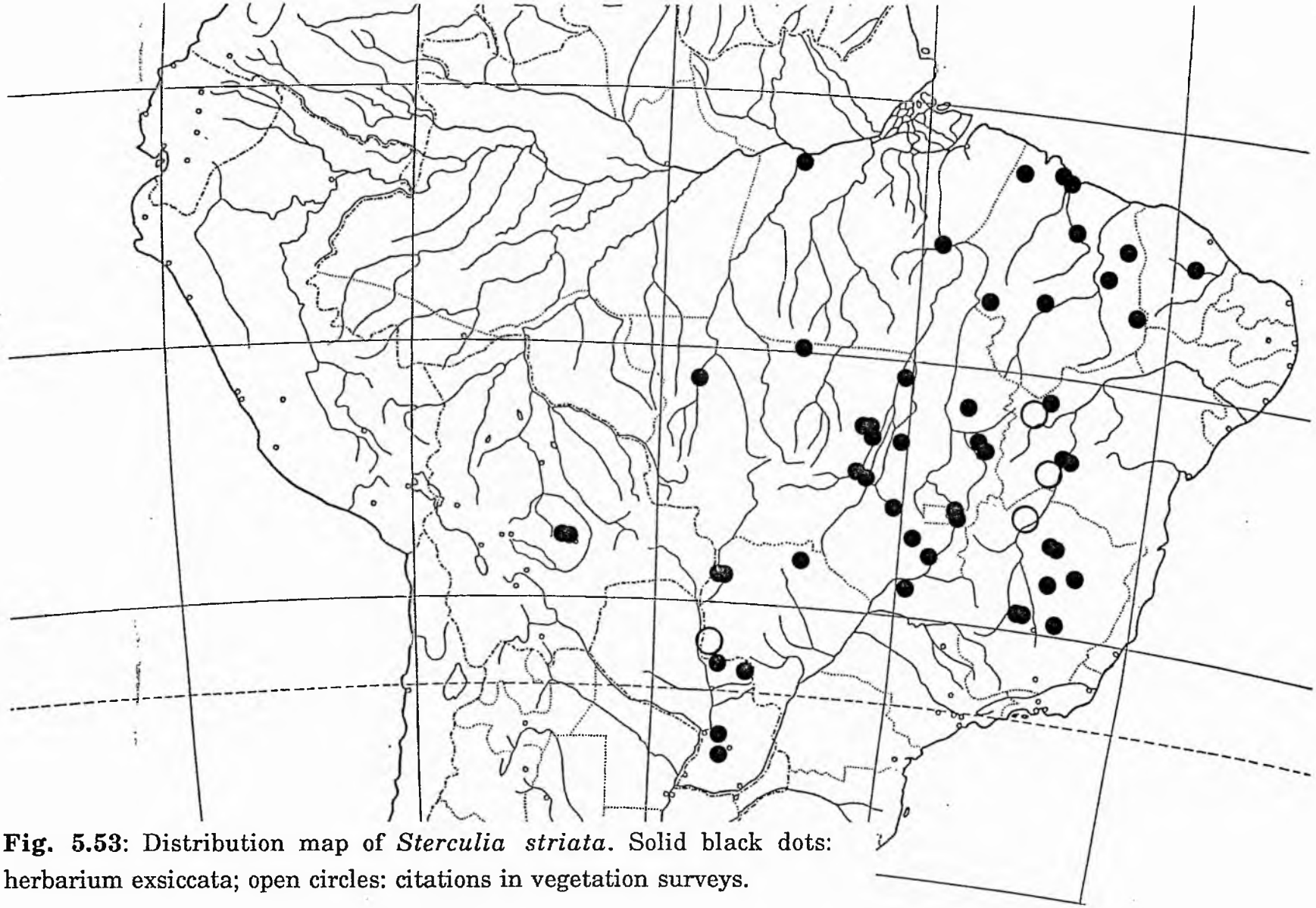


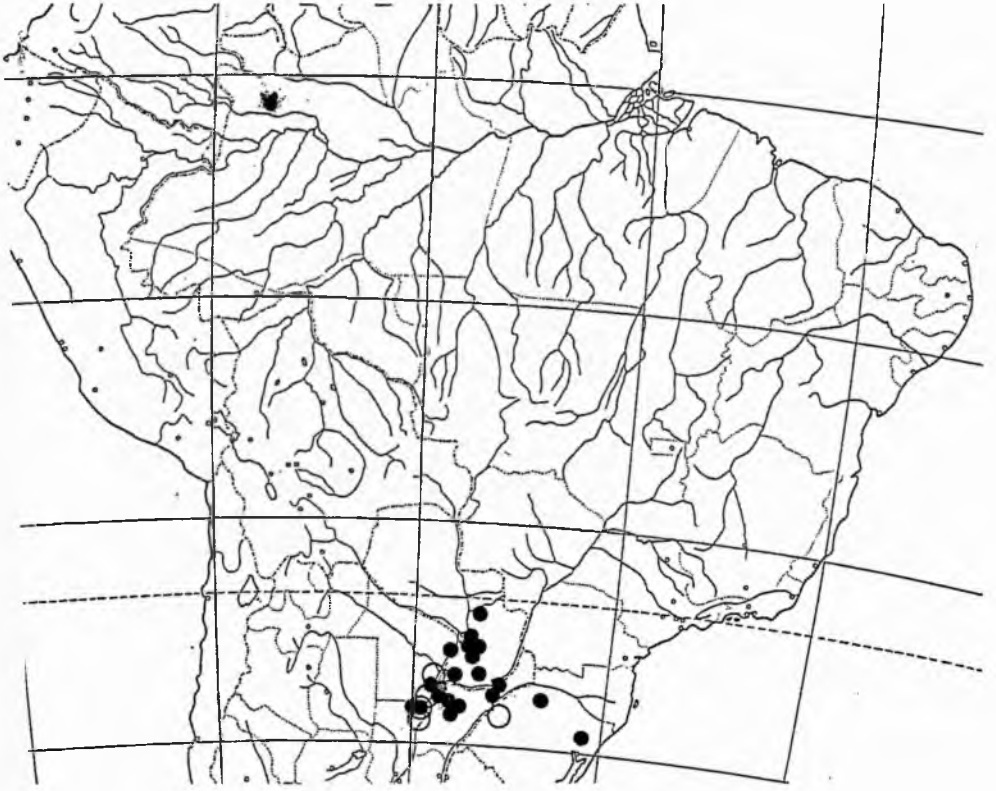
Fig. 5.53: Distribution map of *Sterculia striata*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.54: Distribution map of *Aspidosperma cuspa*.

Fig. 5.55: Distribution map of *Aspidosperma polyneuron*.

Fig. 5.56: Distribution map of *Brunfelsia uniflora*.

Fig. 5.57: Distribution map of *Brunfelsia australis* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



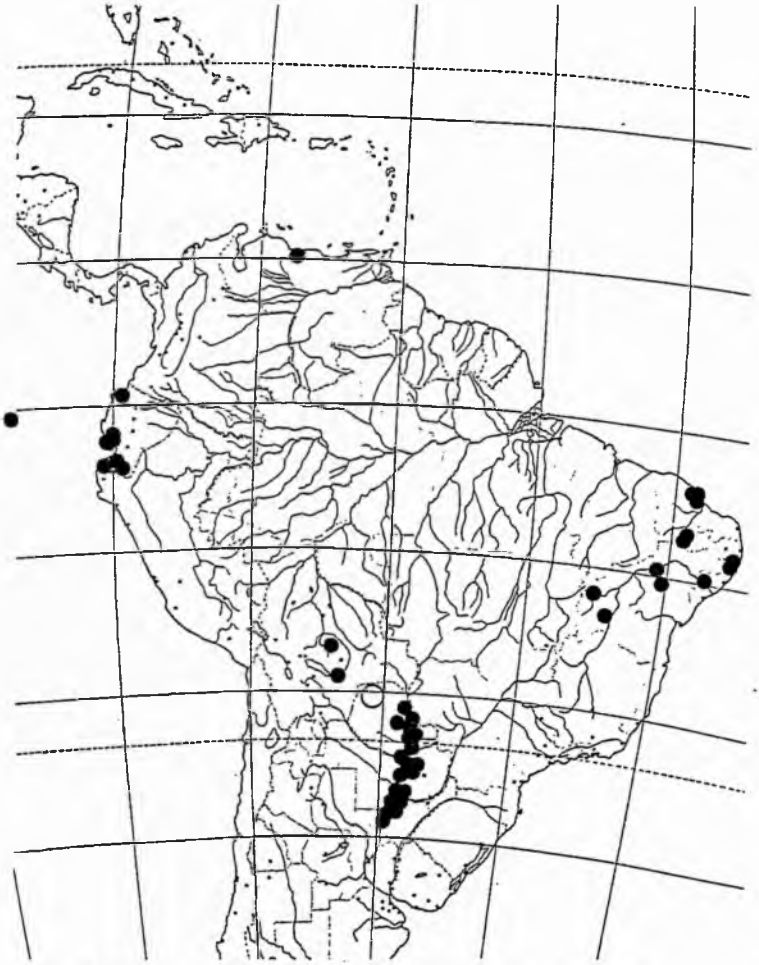


Fig. 5.58: Distribution map of the *Geoffroea striata/spinosa* complex. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

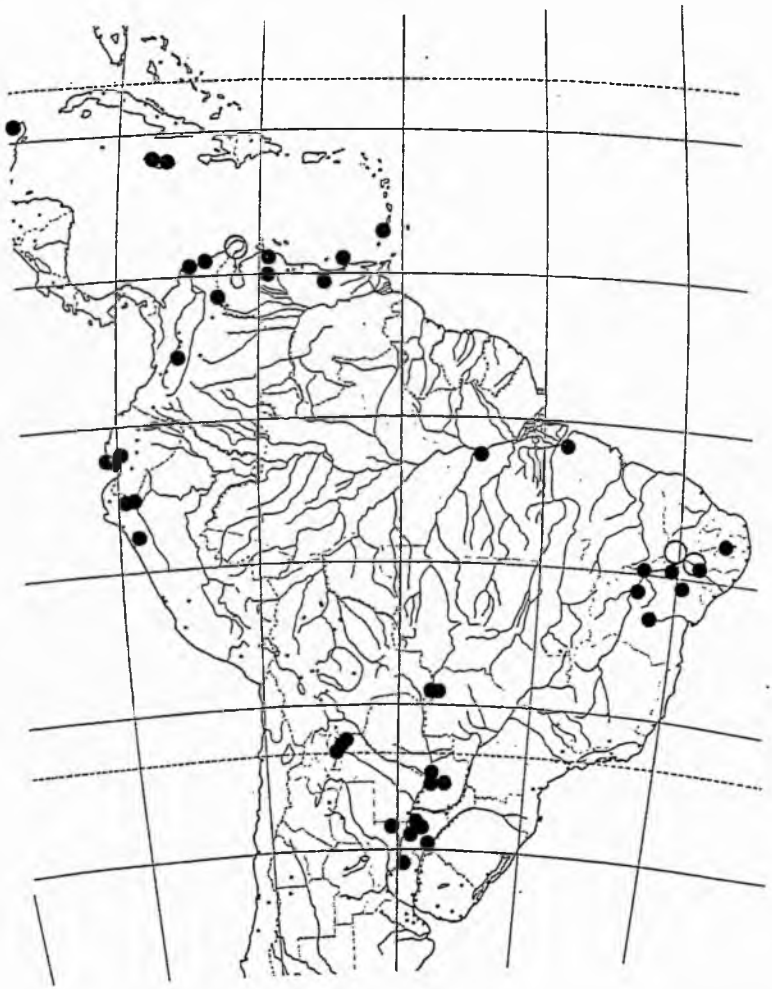


Fig. 5.59: Distribution map of *Ipomoea carnea* ssp. *fistulosa*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

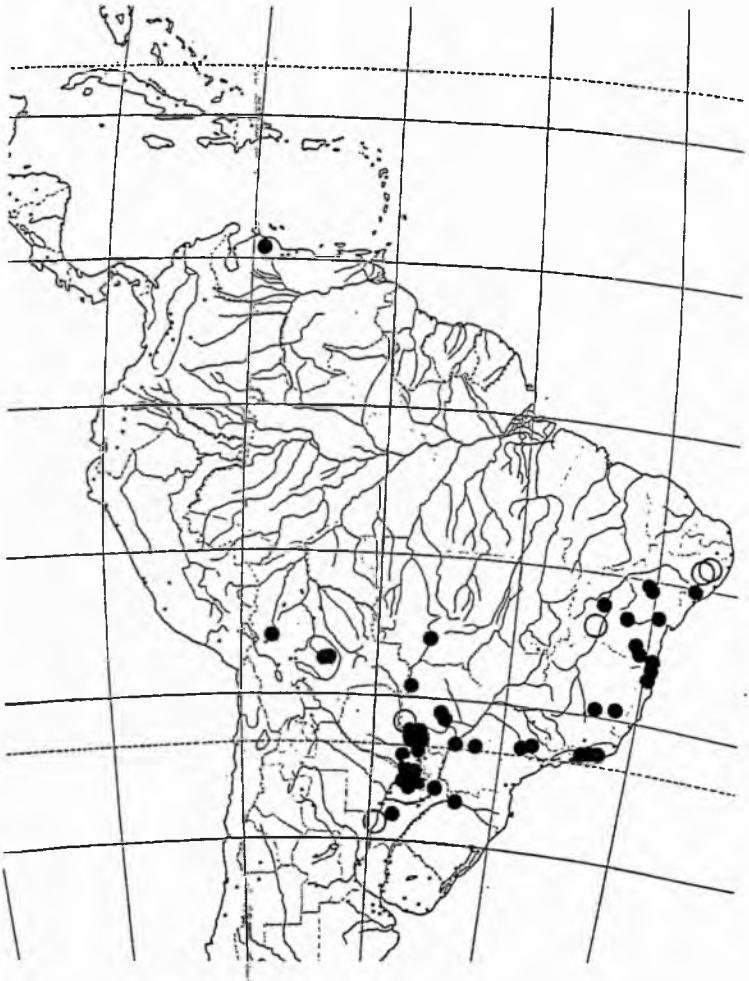


Fig. 5.60: Distribution map of *Peltophorum dubium*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

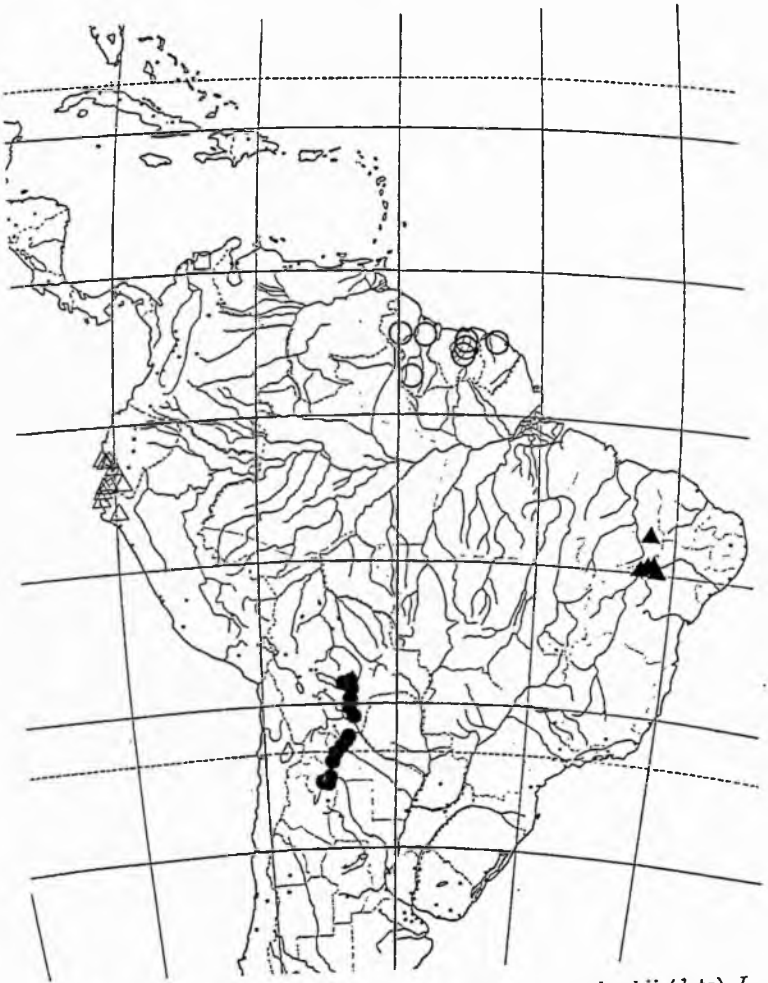


Fig. 5.61: Distribution map of *Loxopterigium grisebachii* (dots), *L. huasango* (open triangles), *L. gutierriezii* (open square), *L. sagotii* (open circles) and *L. gardneri* (solid black triangles).

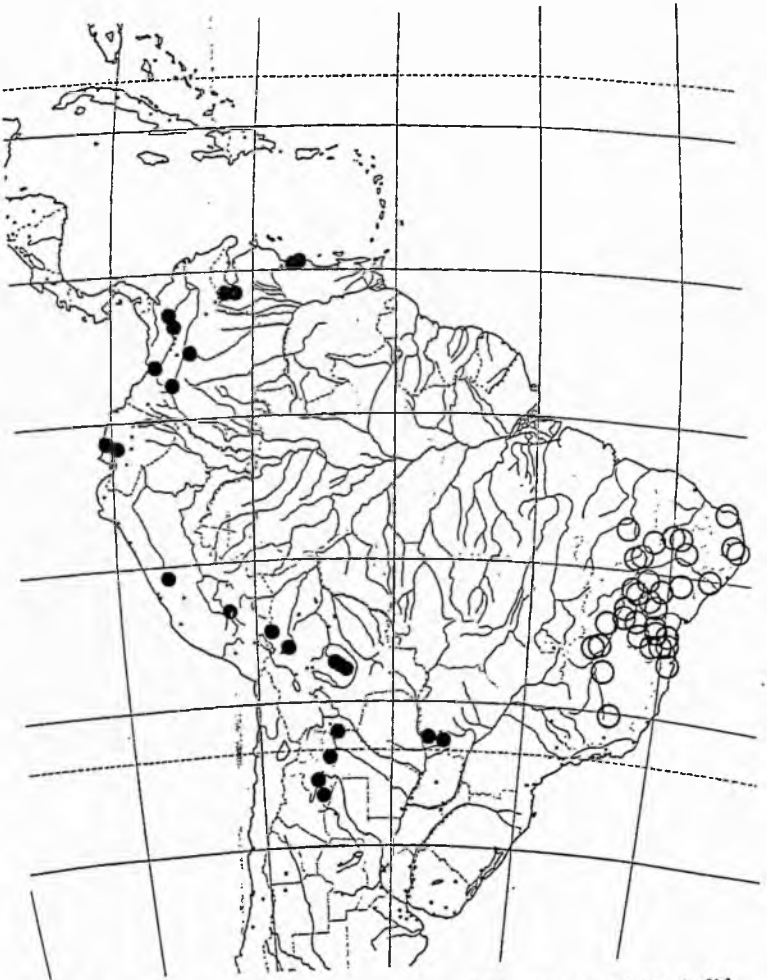


Fig. 5.62: Distribution map of *Senna spectabilis* var. *spectabilis* (solid black dots) and var. *excelsa* (open circles).

Fig. 5.63: Distribution map of *Solanum granuloso-leprosum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.64: Distribution map of the *Cordia alliodora/trichotoma* complex: *C. alliodora* (solid black dots); *C. alliodora?/trichotoma?* (open circles); *C. trichotoma* (solid black triangles: herbarium exsiccata; open triangles: citations in vegetation surveys).

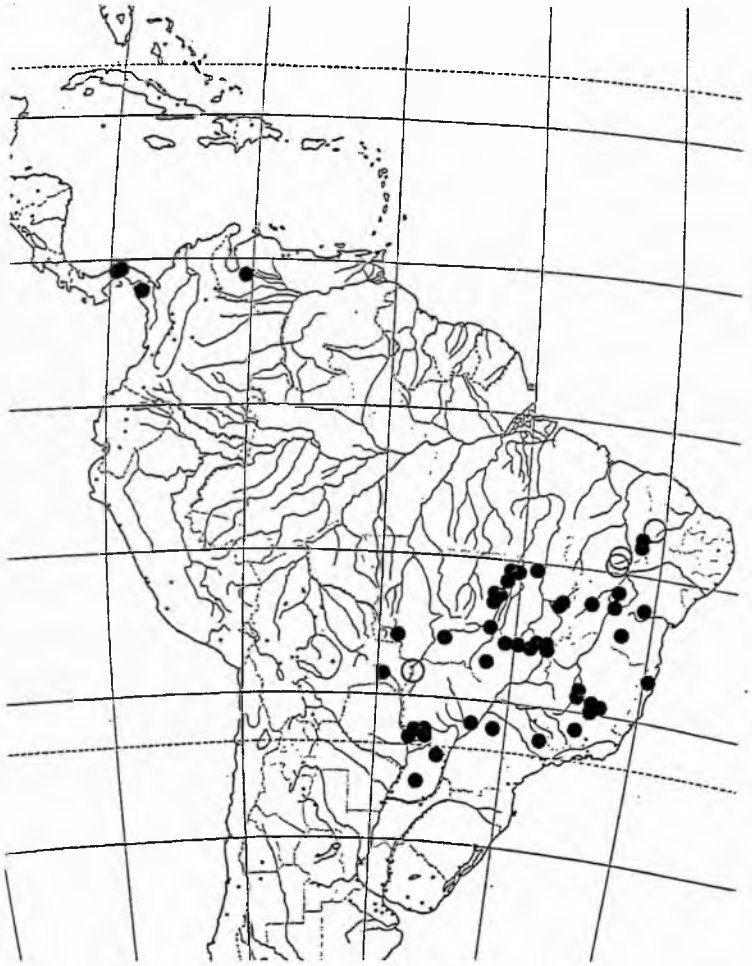


Fig. 5.65: Distribution map of *Platypodium elegans* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

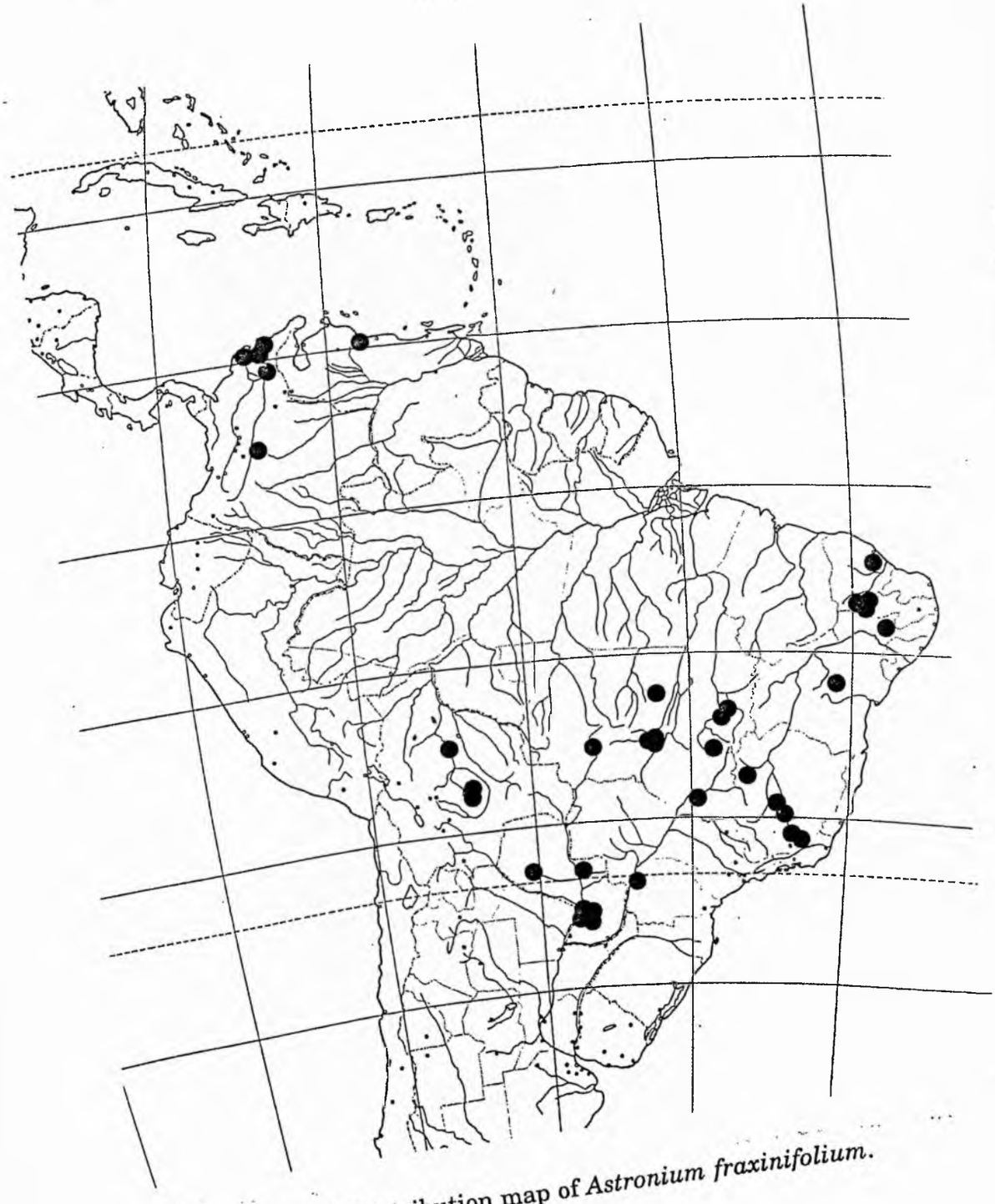


Fig. 5.66: Distribution map of *Astronium fraxinifolium*.

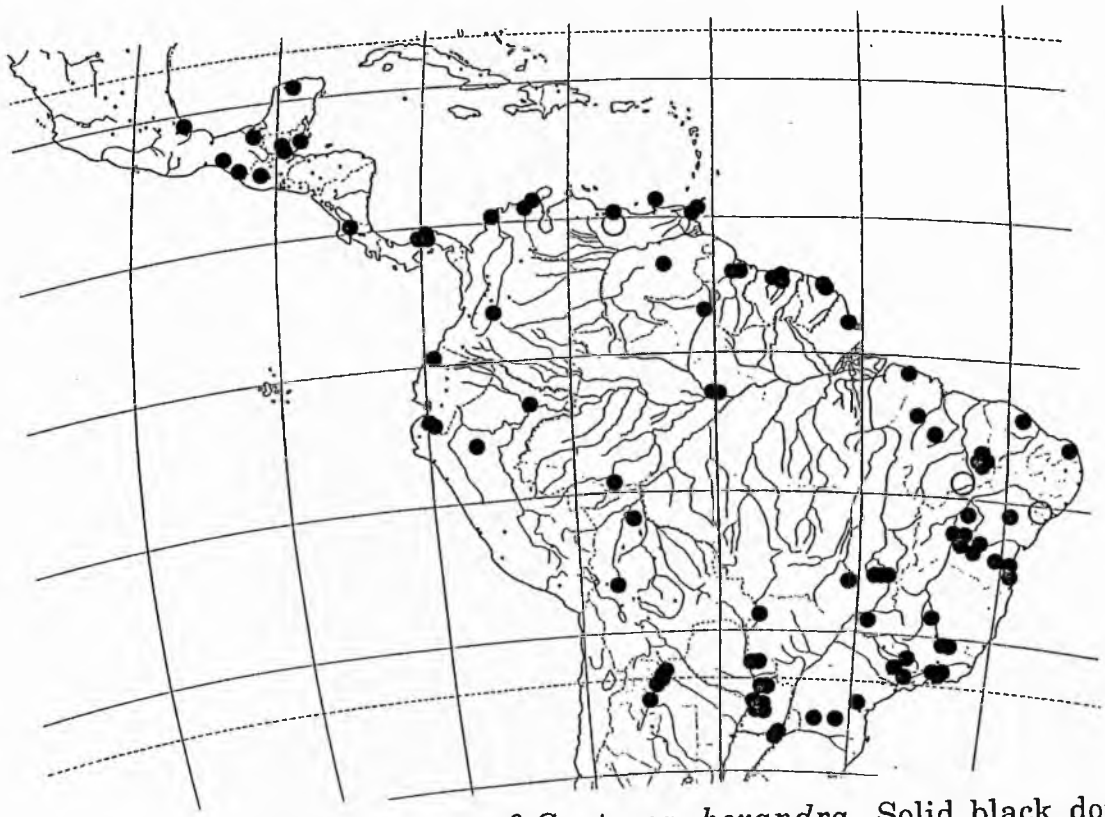
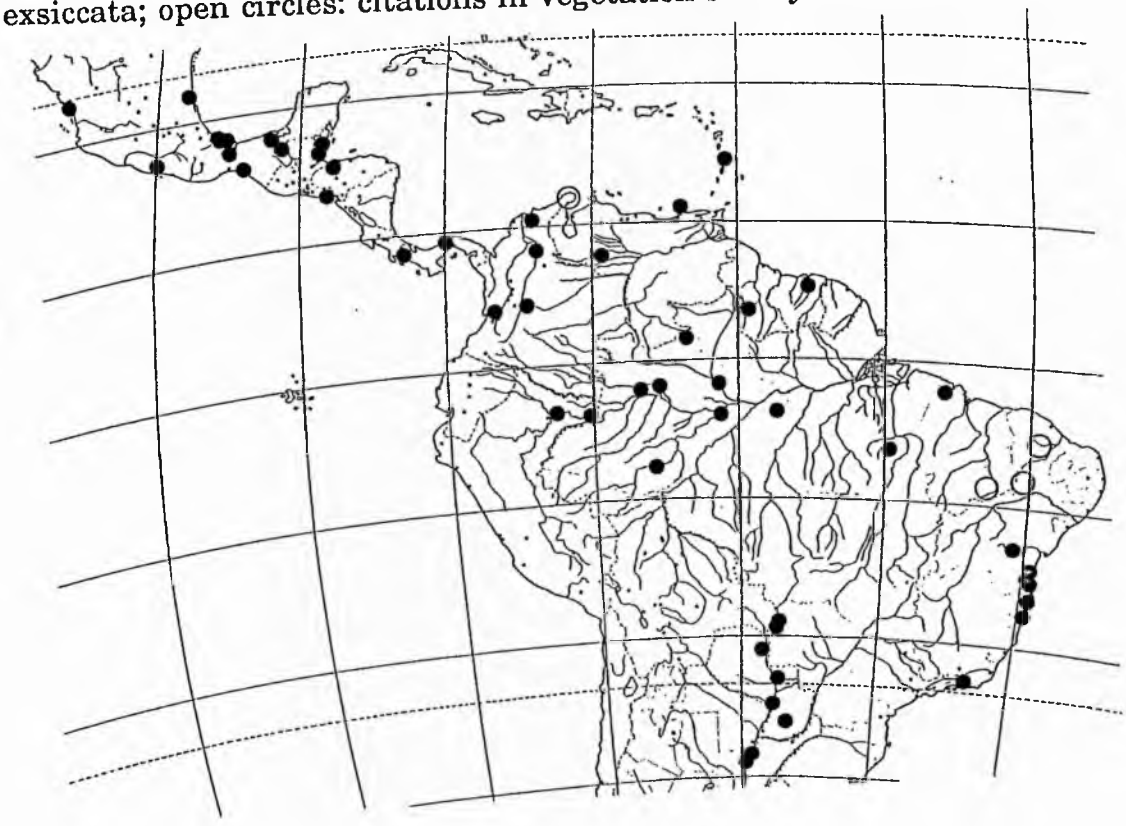


Fig. 5.67: Distribution map of *Coutarea hexandra*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.68: Distribution map of *Crateva tapia*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



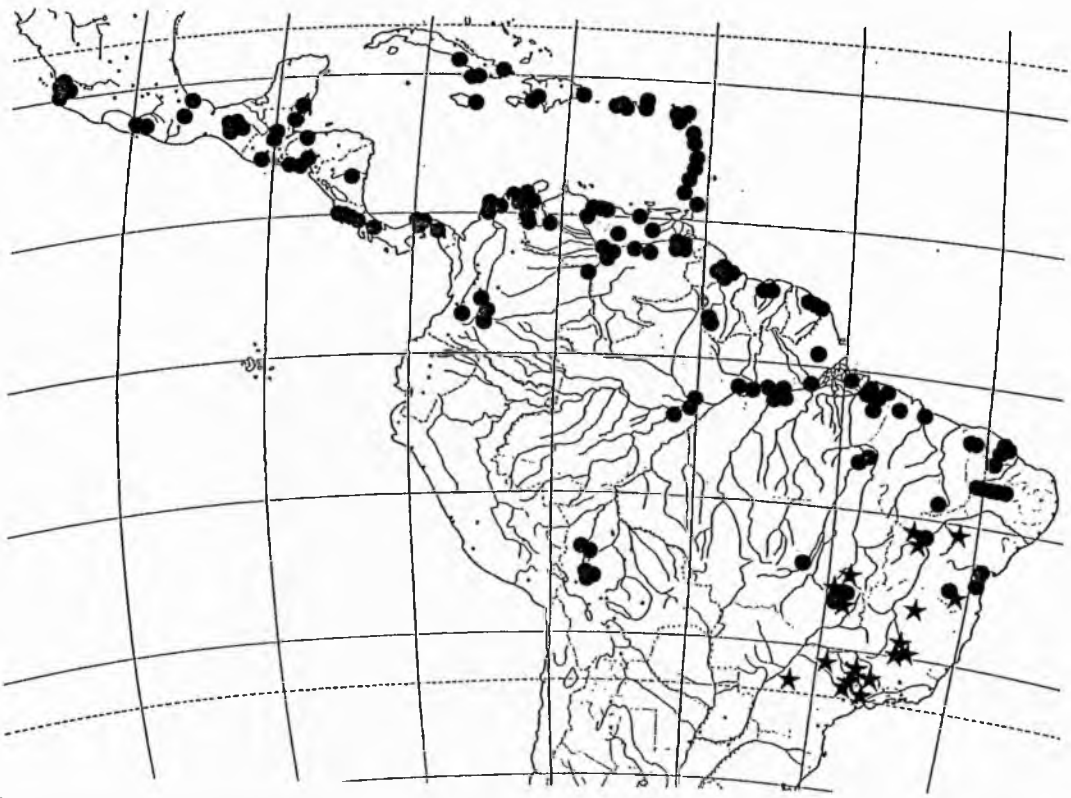
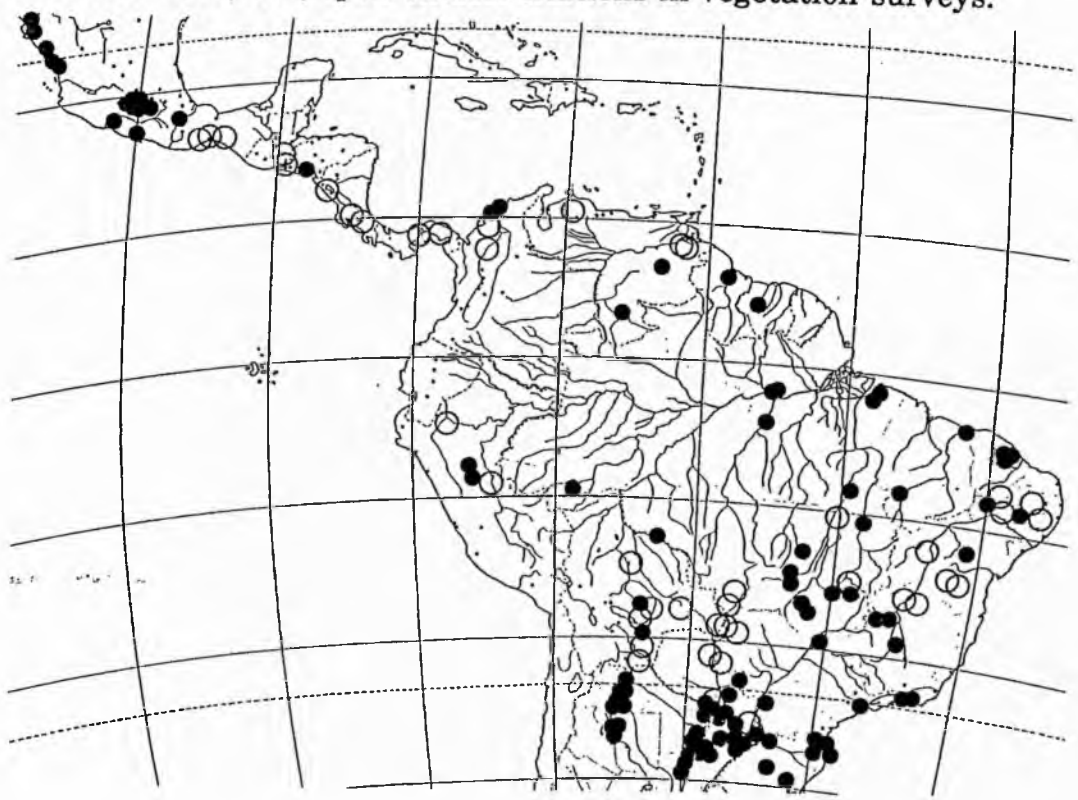


Fig. 5.69: Distribution map of *Hymenaea courbaril* var. *courbaril* (dots) and var. *stilbocarpa* (stars).

Fig. 5.70: Distribution map of *Tabebuia impetiginosa*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



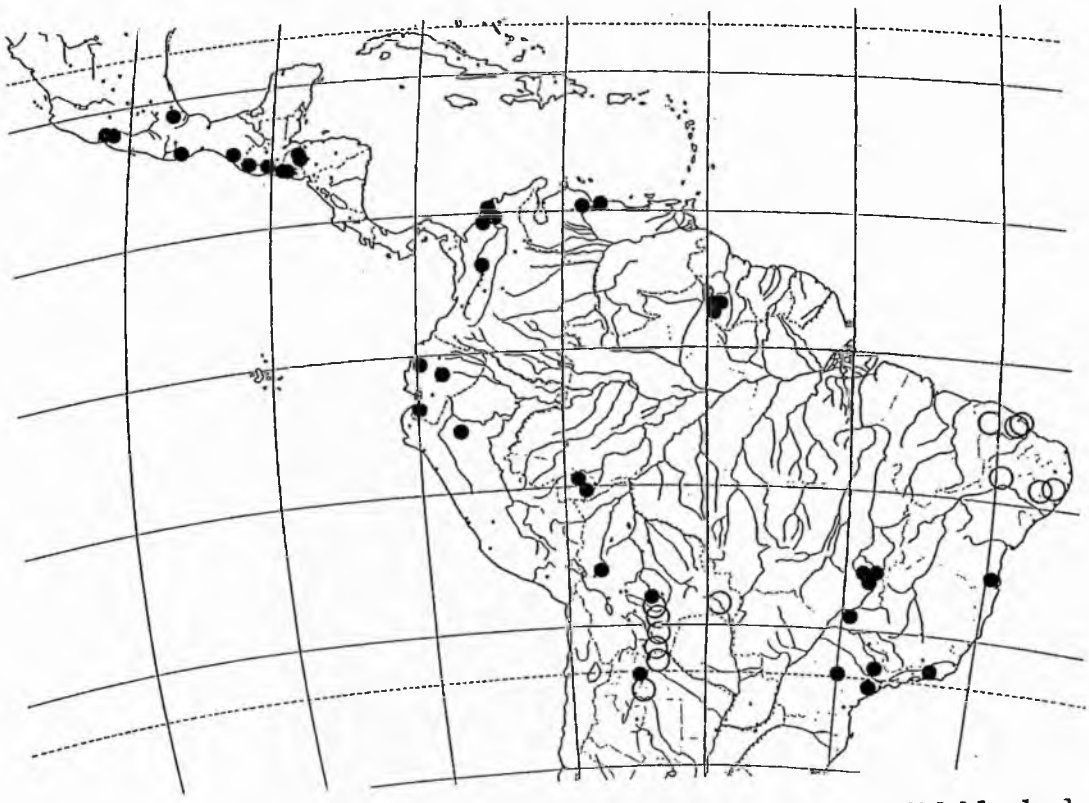
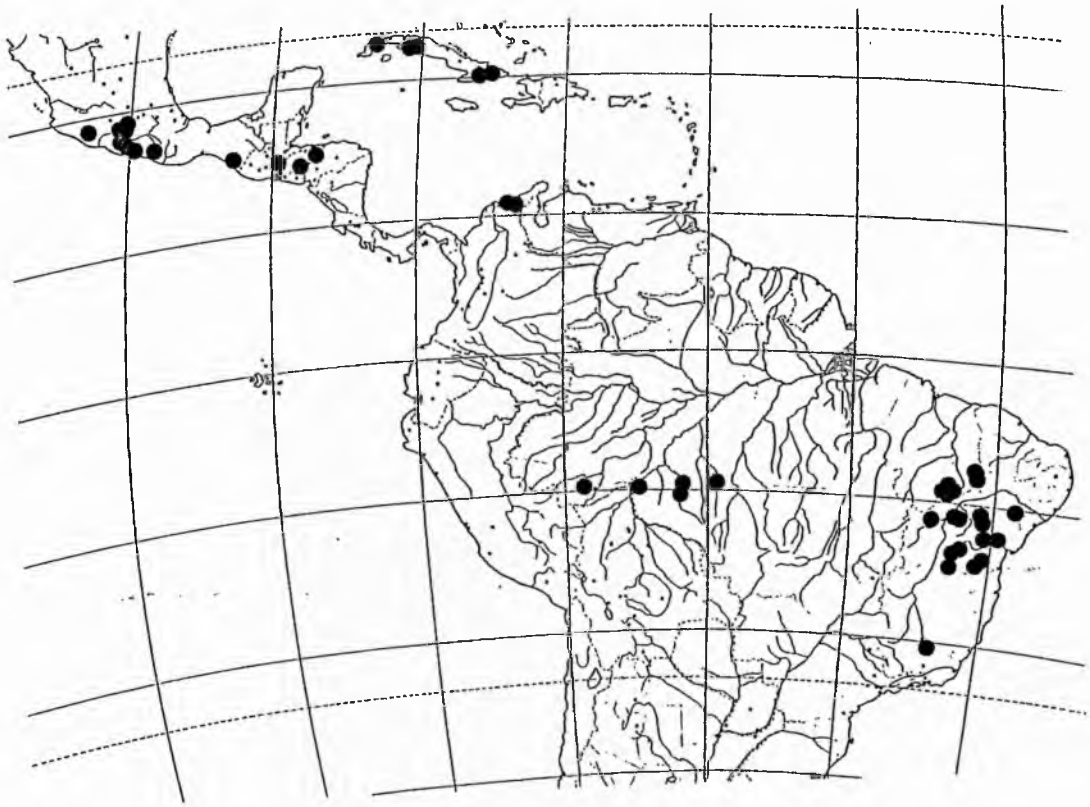


Fig. 5.71: Distribution map of *Myroxylon balsamum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.72: Distribution map of *Poeppigia procera*.



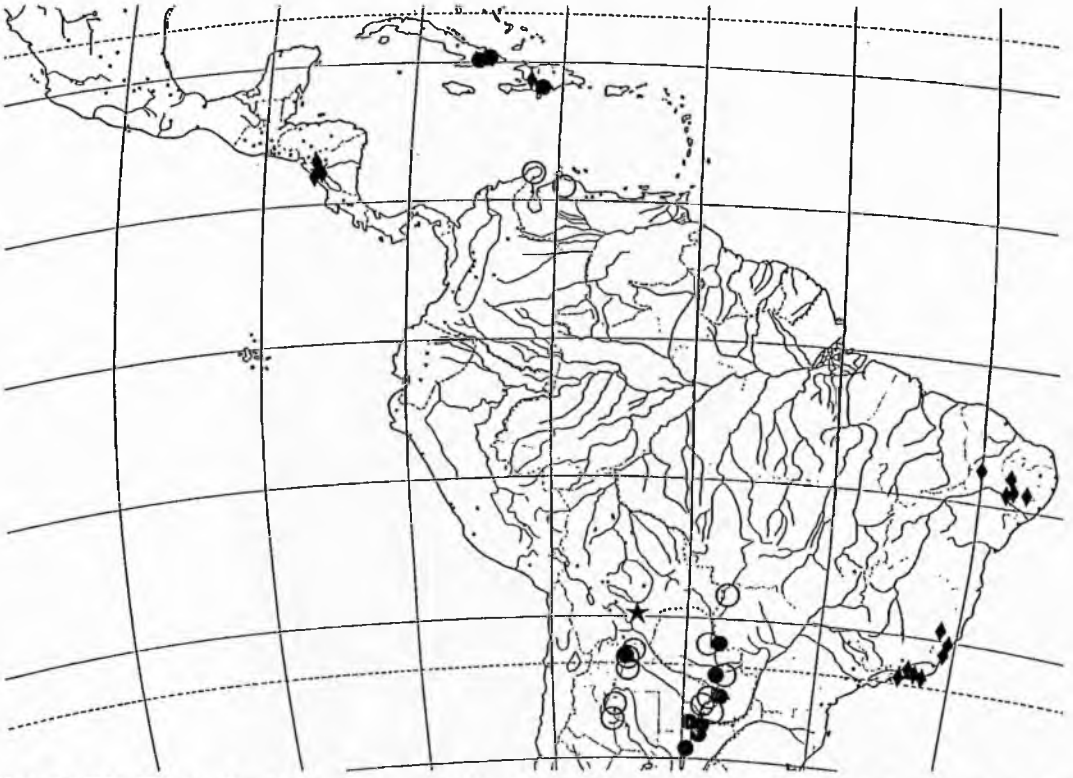
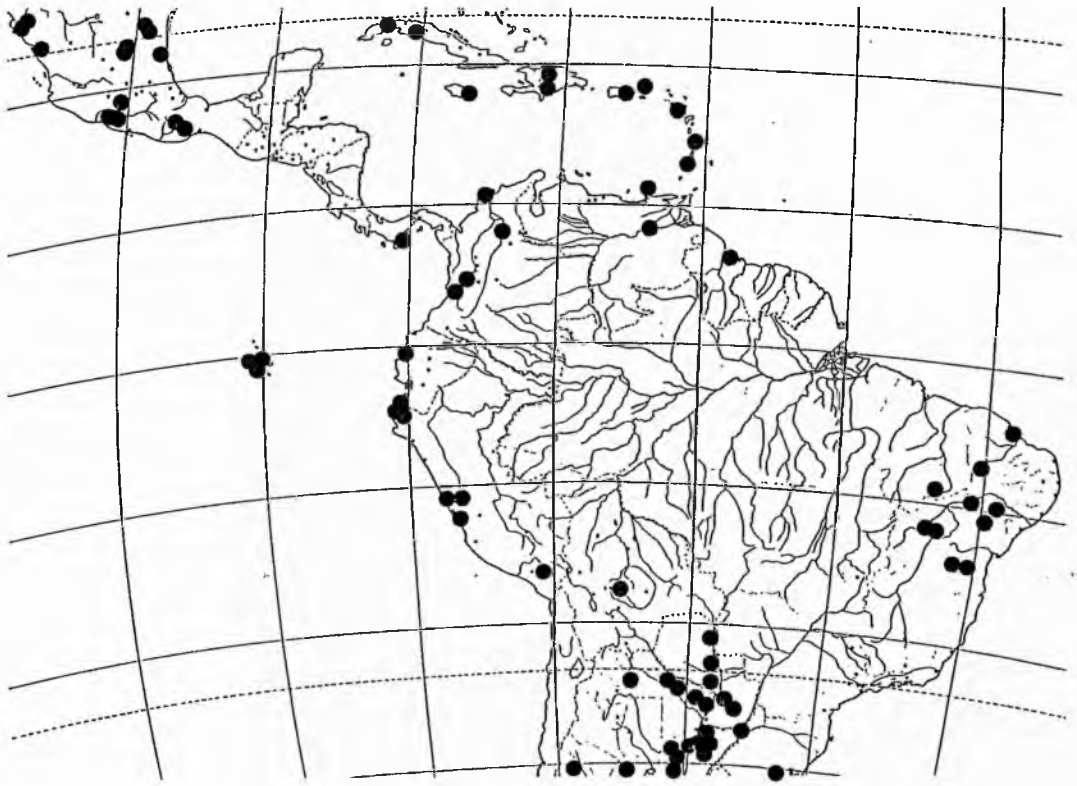


Fig. 5.73: Distribution map of *Phyllostylon rhamnoides* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys), *P. brasiliense* (diamonds) and *P. orthopterum* (star).

Fig. 5.74: Distribution map of *Parkinsonia aculeata*.



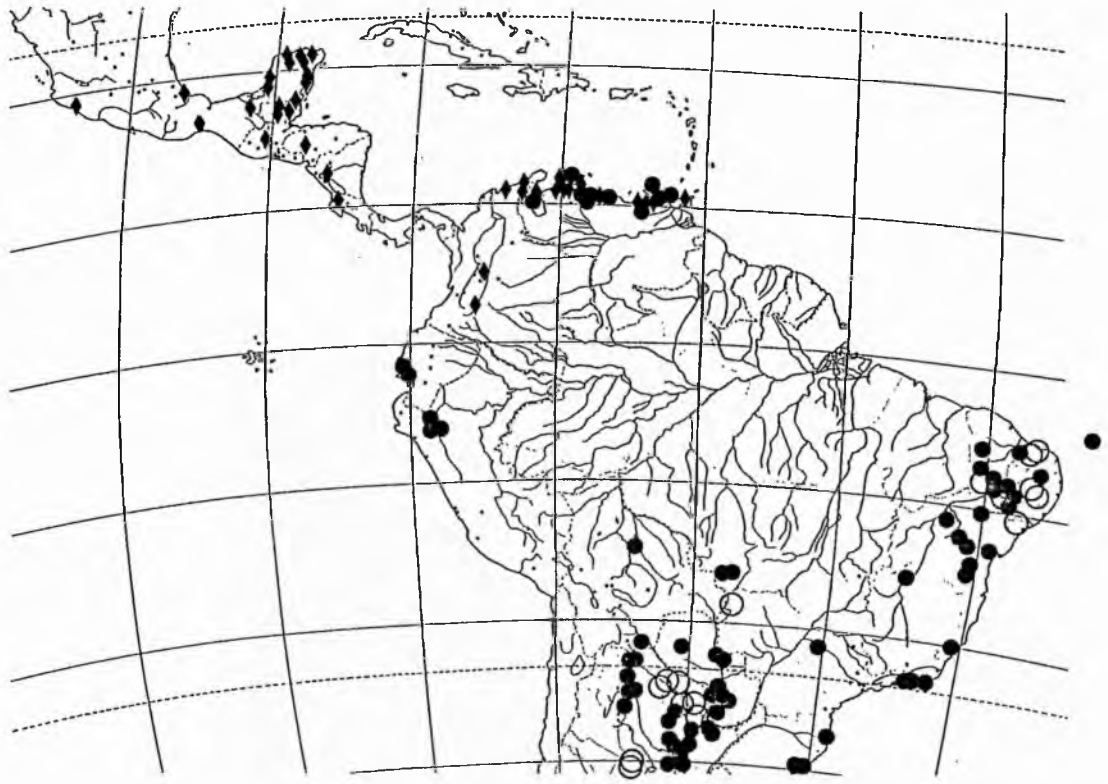
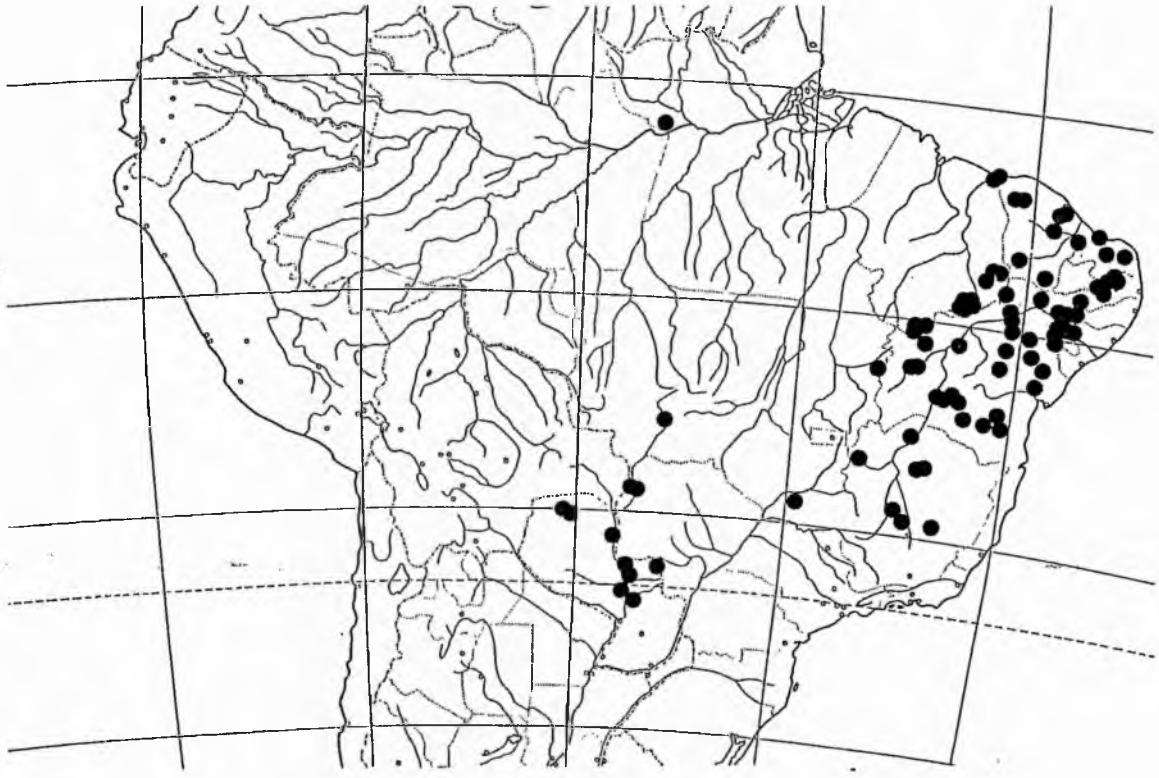


Fig. 5.75: Distribution map of *Sideroxylon obtusifolium* ssp. *obtusifolium* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and ssp. *buxifolium* (diamonds).

Fig. 5.76: Distribution map of *Aspidosperma pyrifolium*.



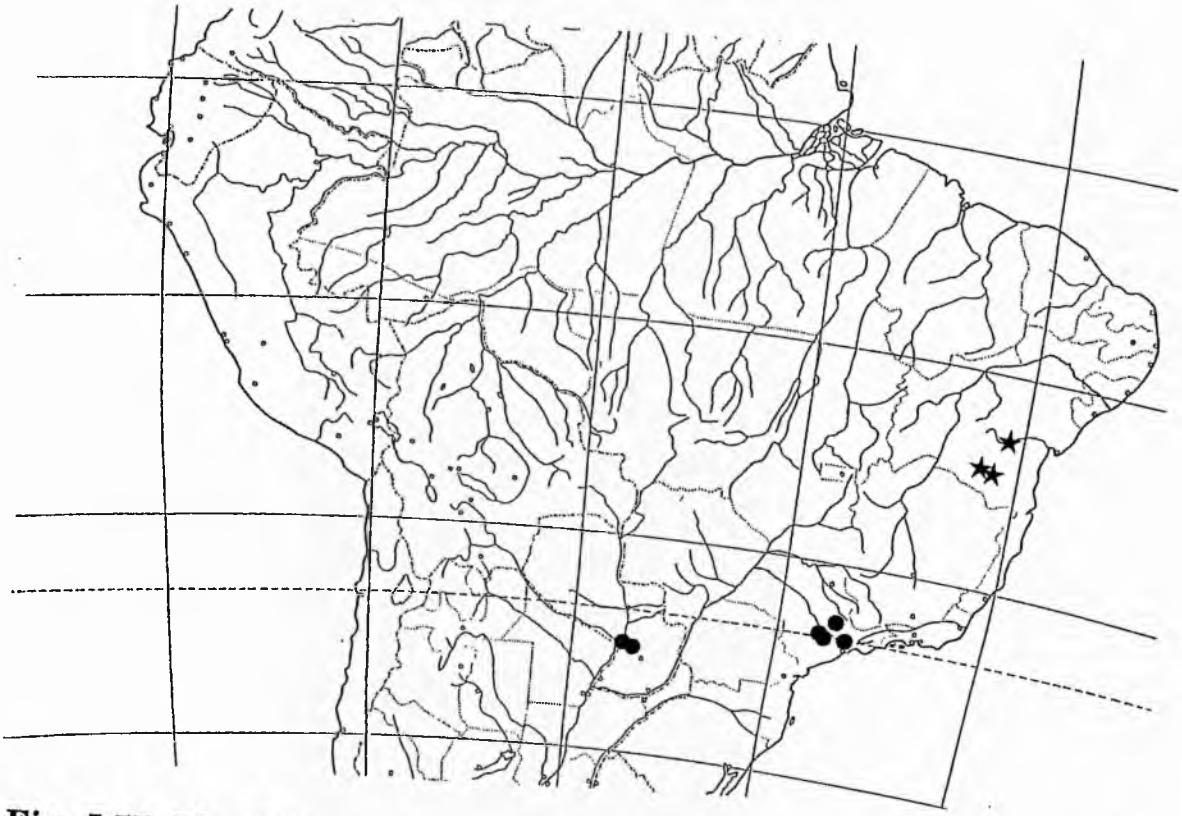
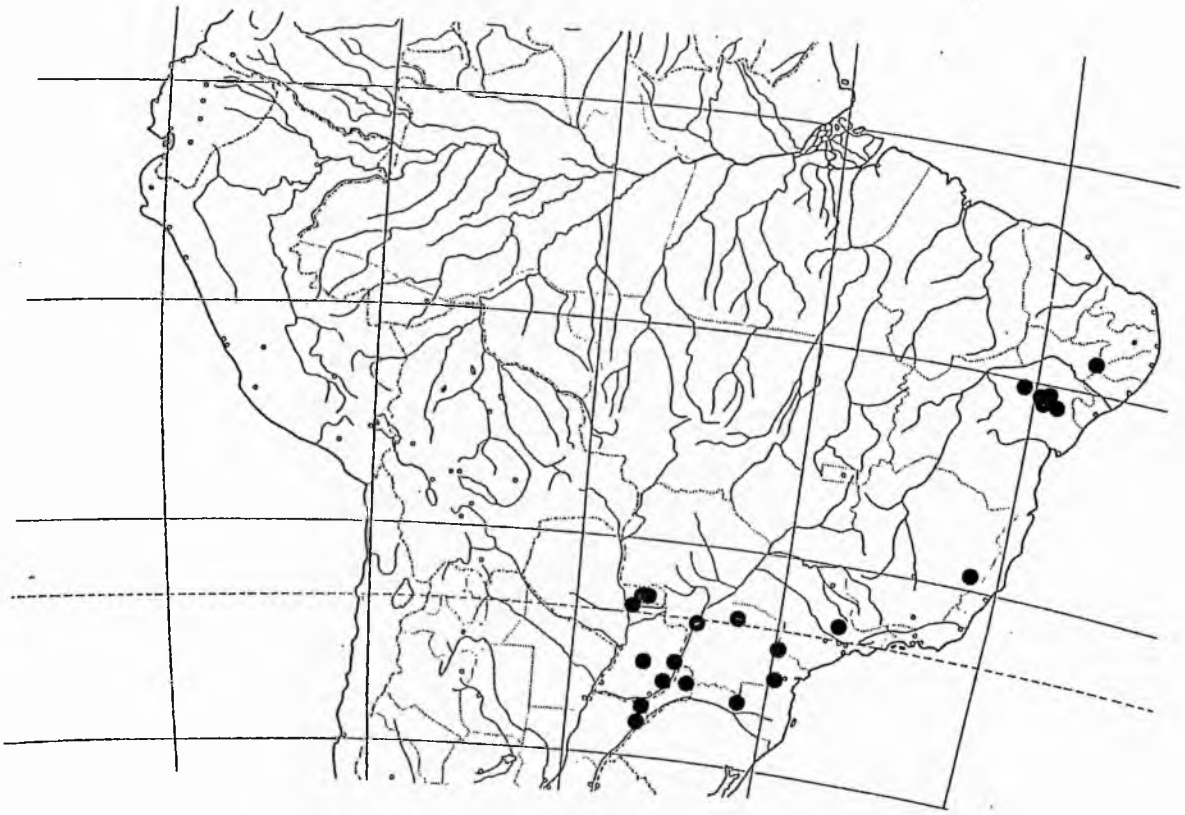


Fig. 5.77: Distribution map of *Aspidosperma riedelii* ssp. *riedelii* (dots) and ssp. *oliganthum* (stars).

Fig. 5.78: Distribution map of *Balfourodendron riedelianum*.



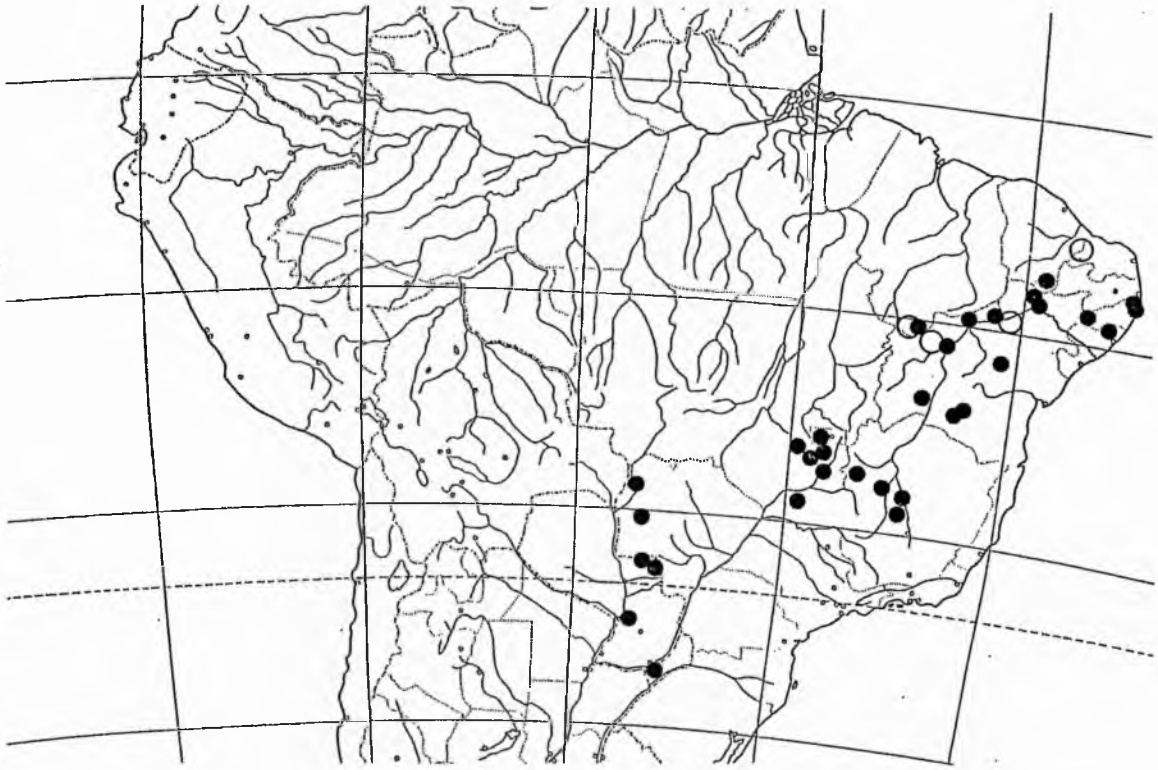
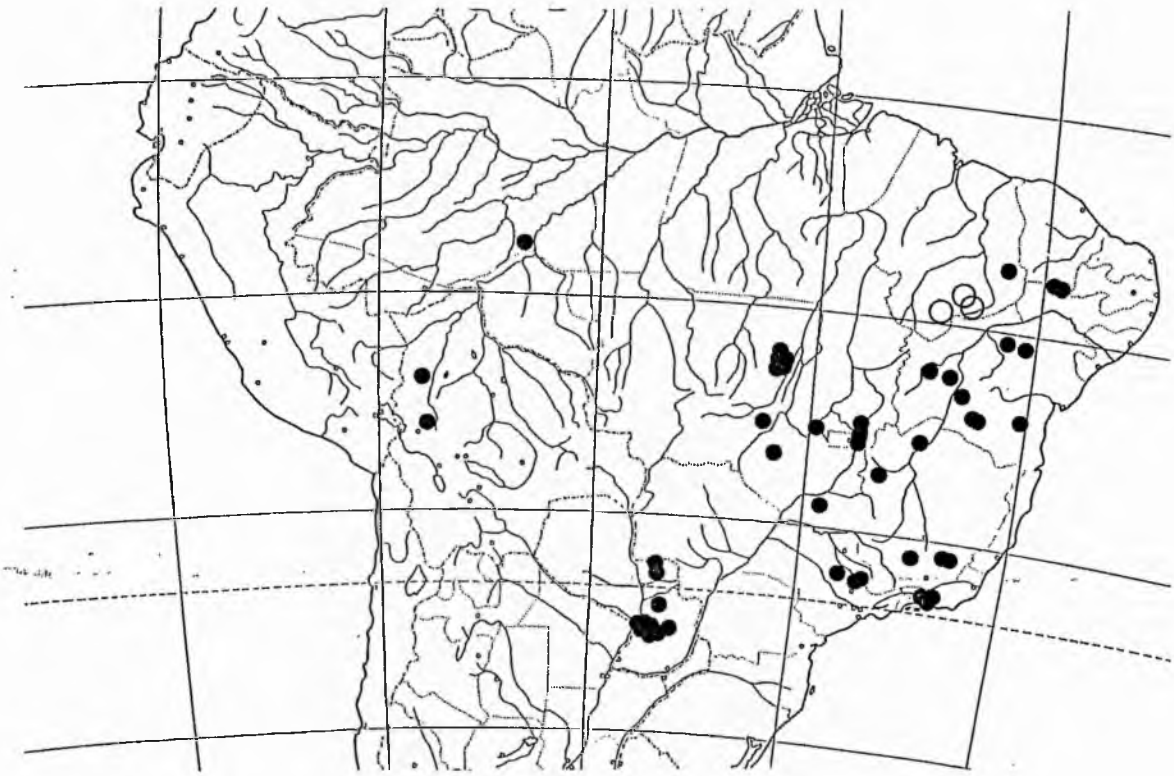


Fig. 5.79: Distribution map of *Hymenaea martiana*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.80: Distribution map of *Machaerium acutifolium*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



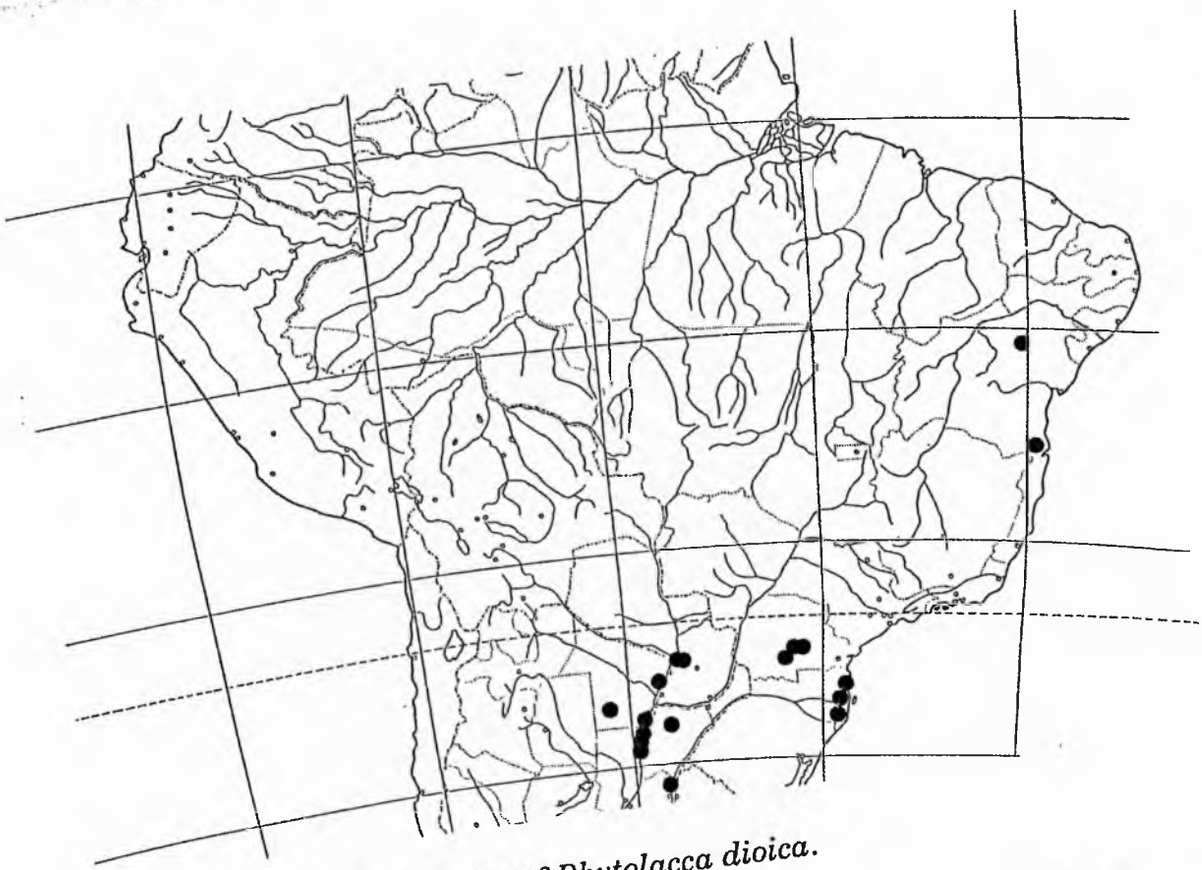
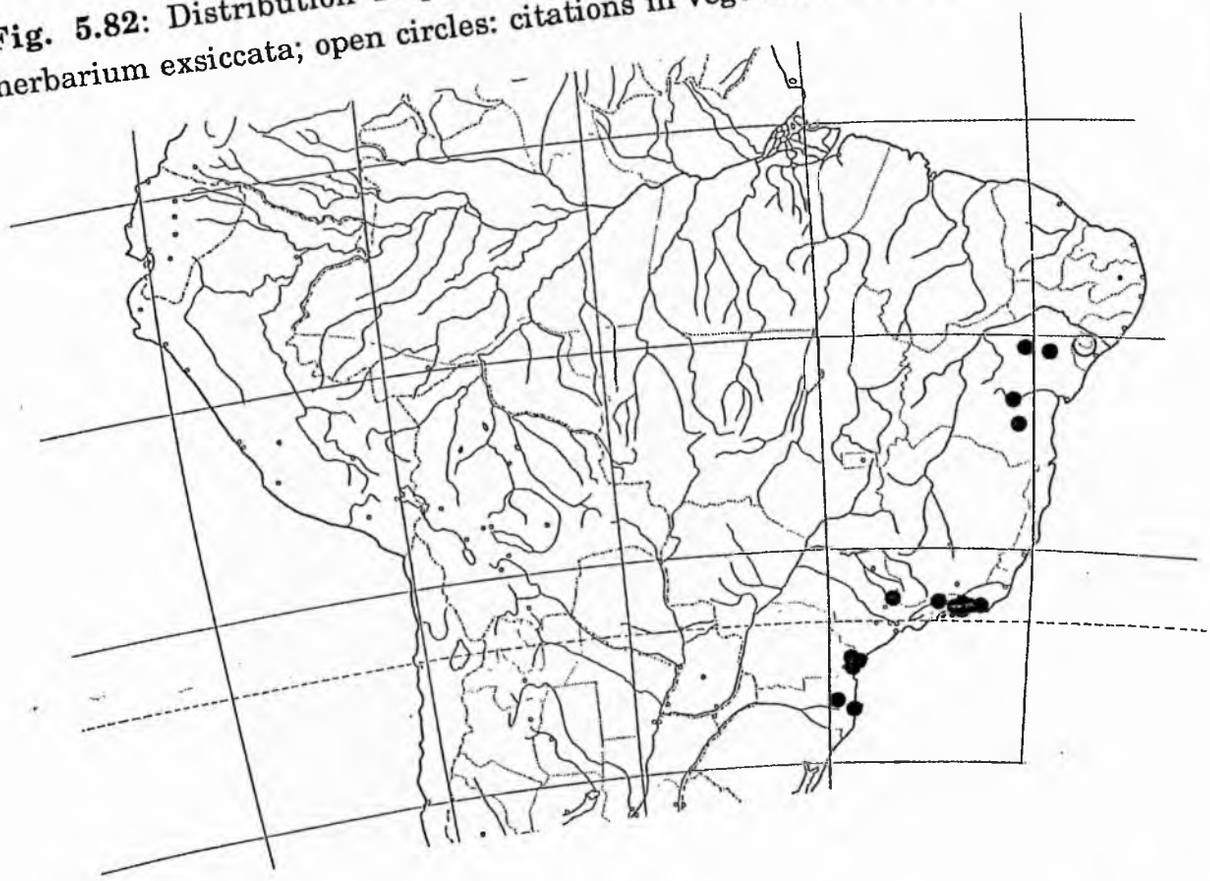


Fig. 5.81: Distribution map of *Phytolacca dioica*.

Fig. 5.82: Distribution map of *Alseis floribunda*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



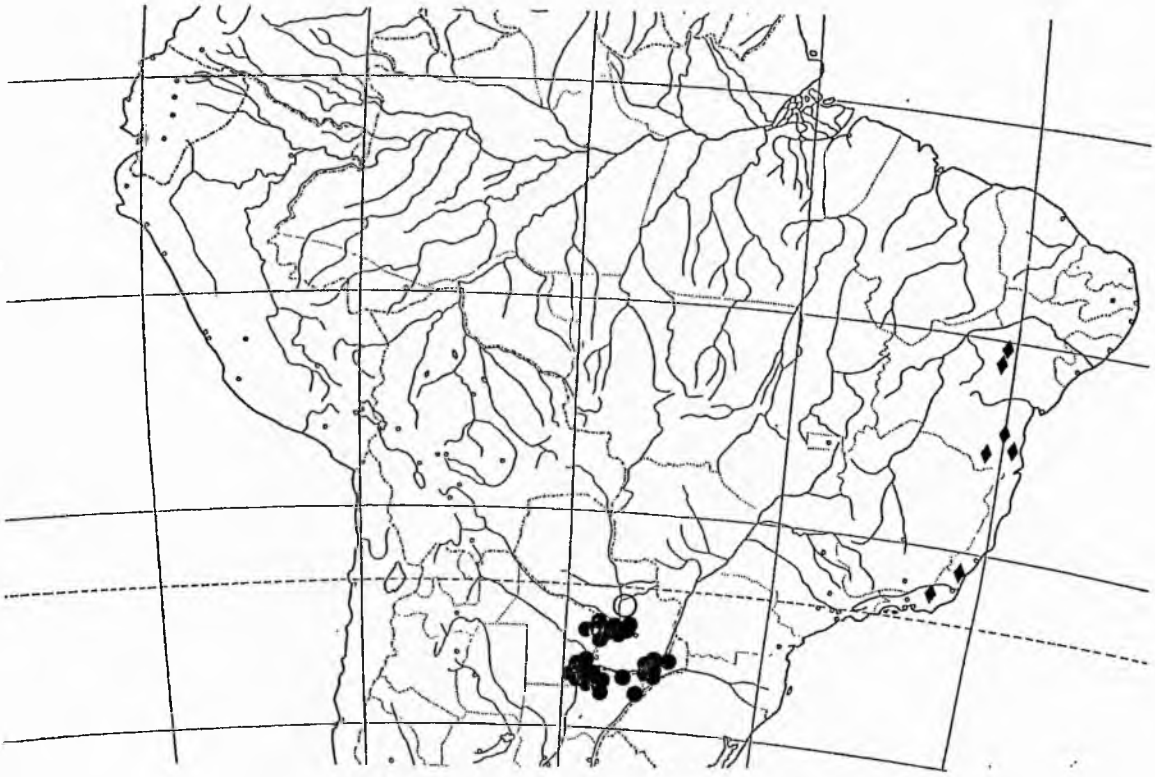
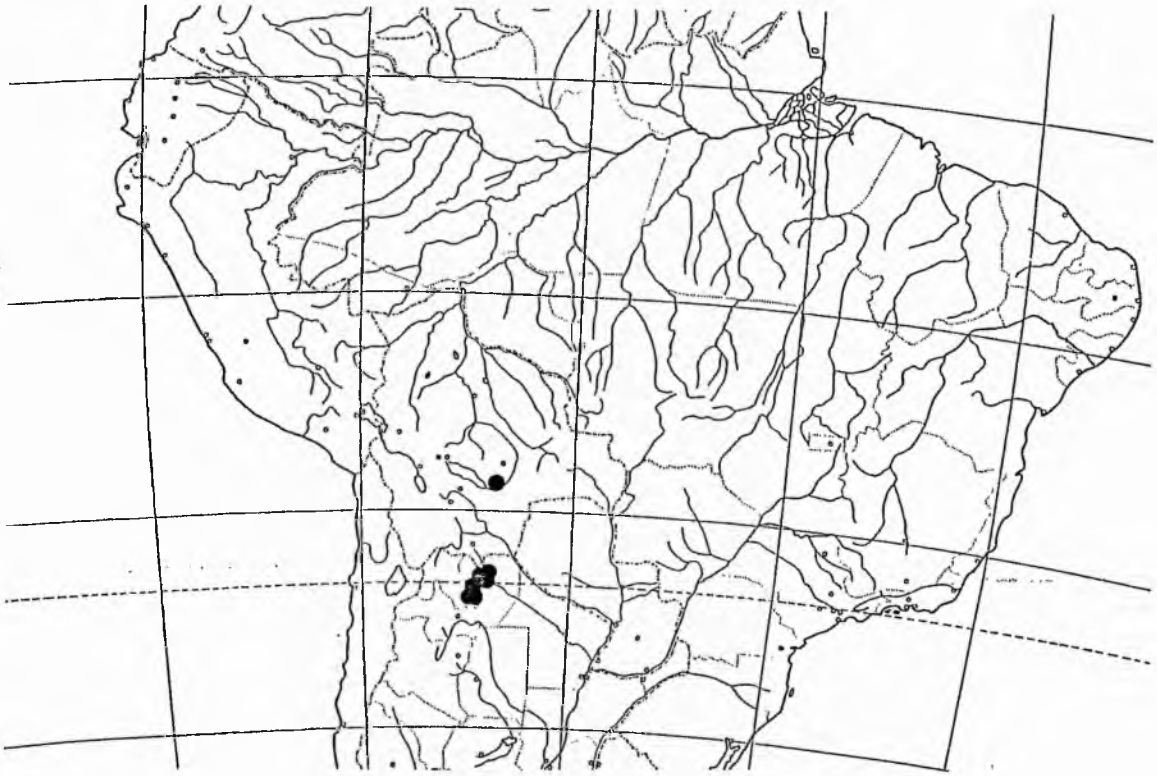


Fig. 5.83: Distribution map of *Astronium balansae* (solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys) and *A. concinnum* (diamonds).

Fig. 5.84: Distribution map of *Athyana weinmannifolia*.



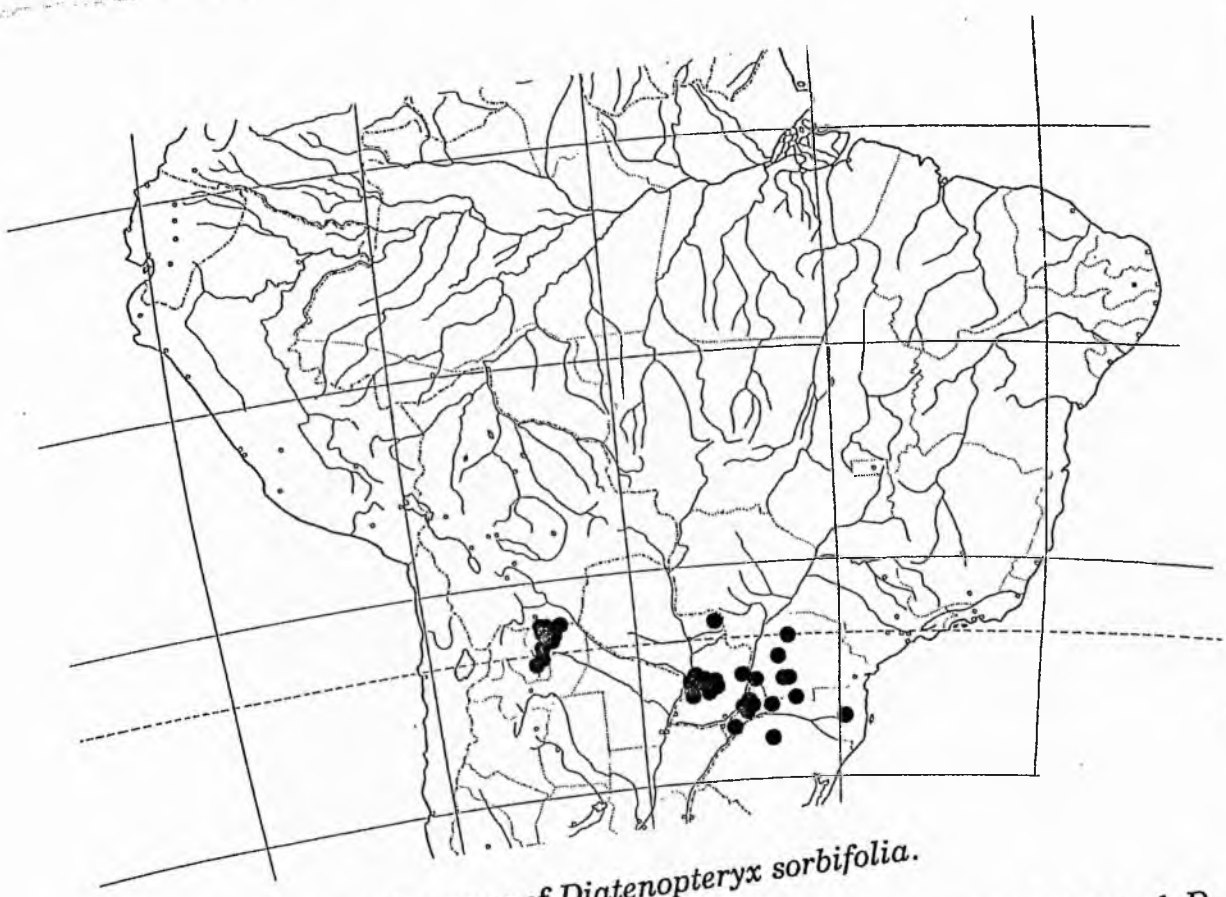
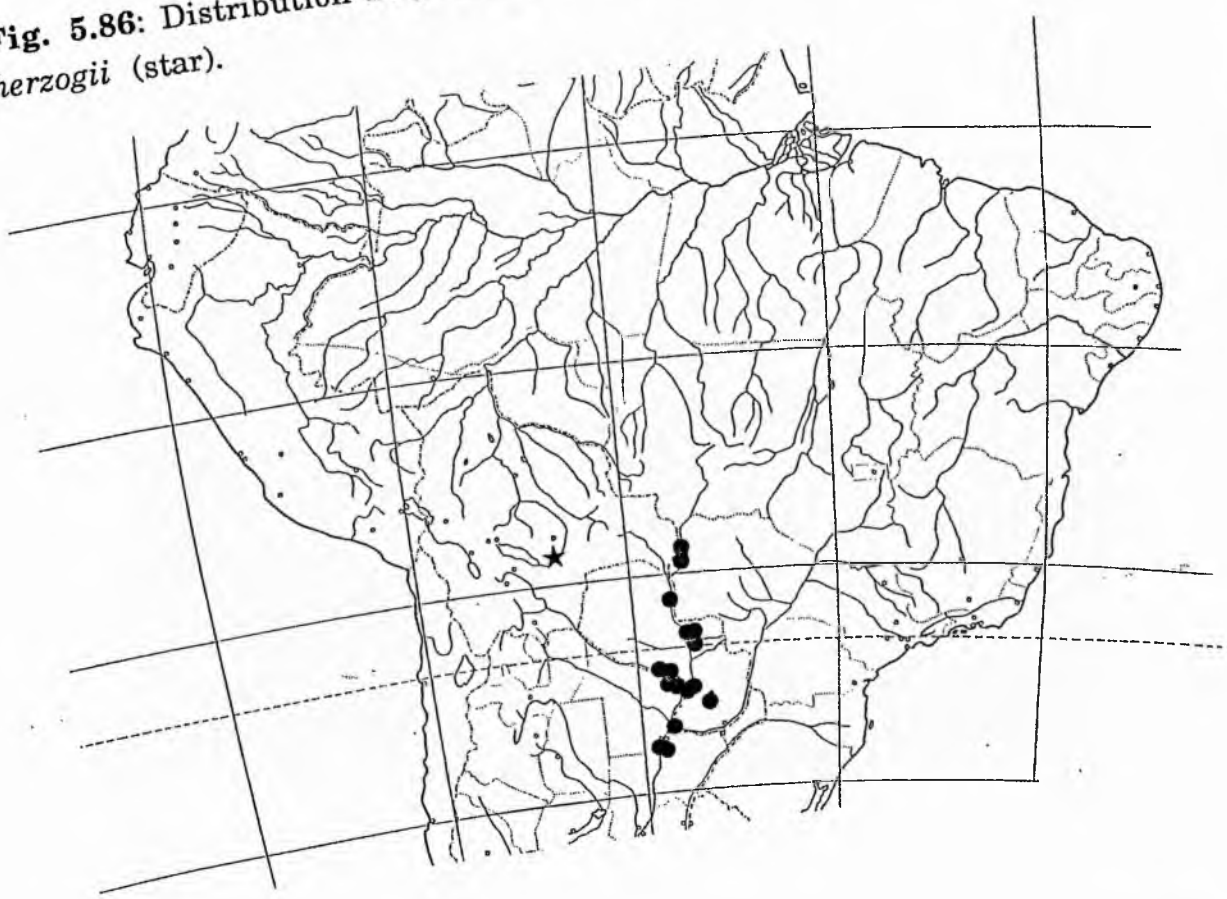


Fig. 5.85: Distribution map of *Diatenopteryx sorbifolia*.

Fig. 5.86: Distribution map of *Diplokeleba floribunda* (dots) and *D. herzogii* (star).



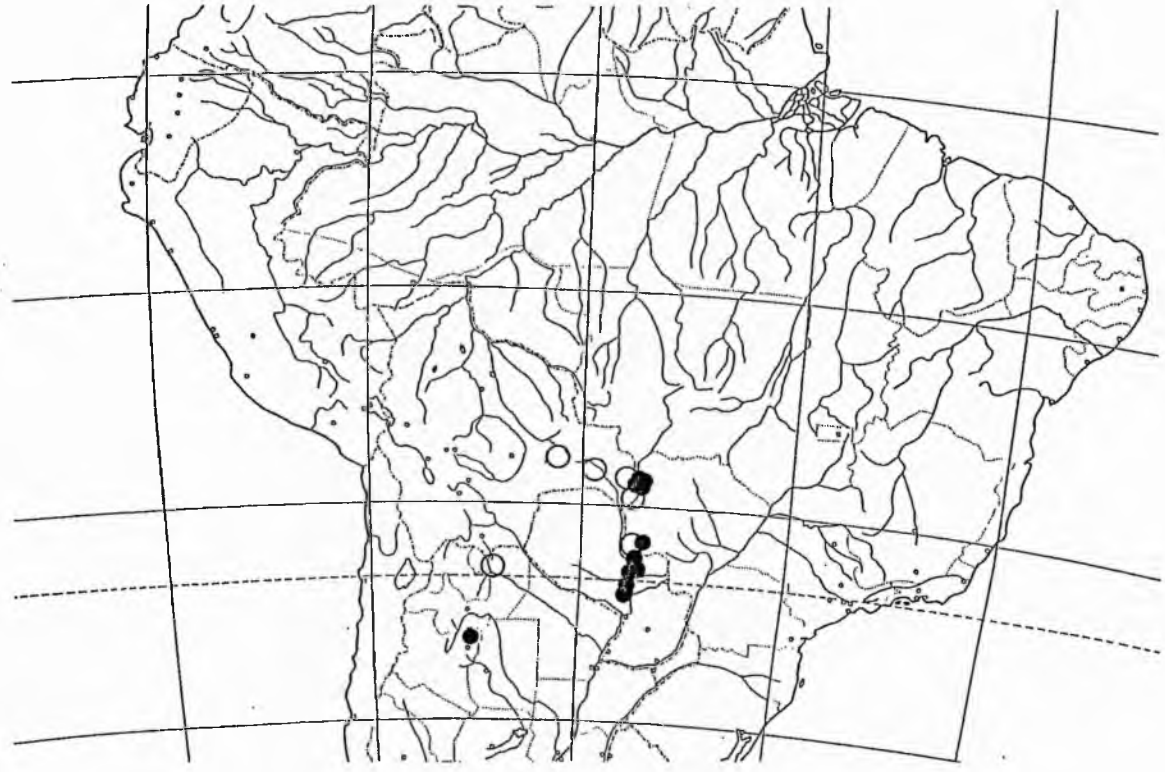
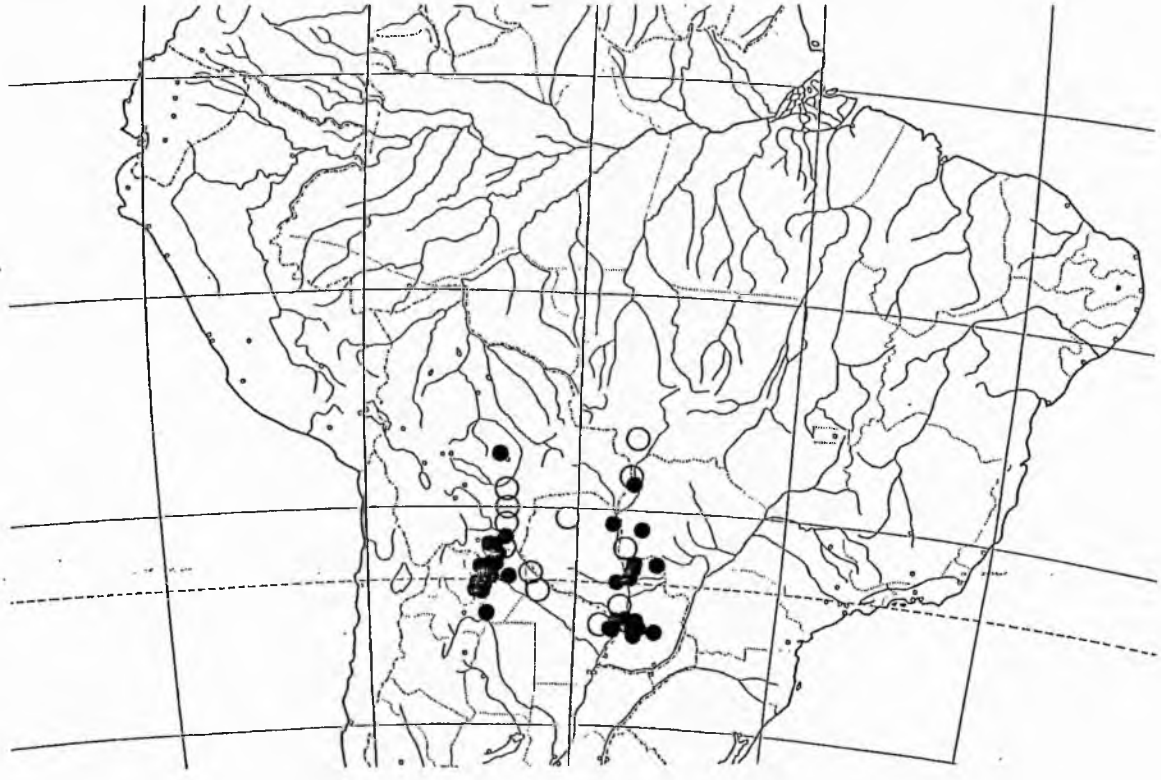


Fig. 5.87: Distribution map of *Ziziphus oblongifolius* . Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.88: Distribution map of *Calycophyllum multiflorum*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



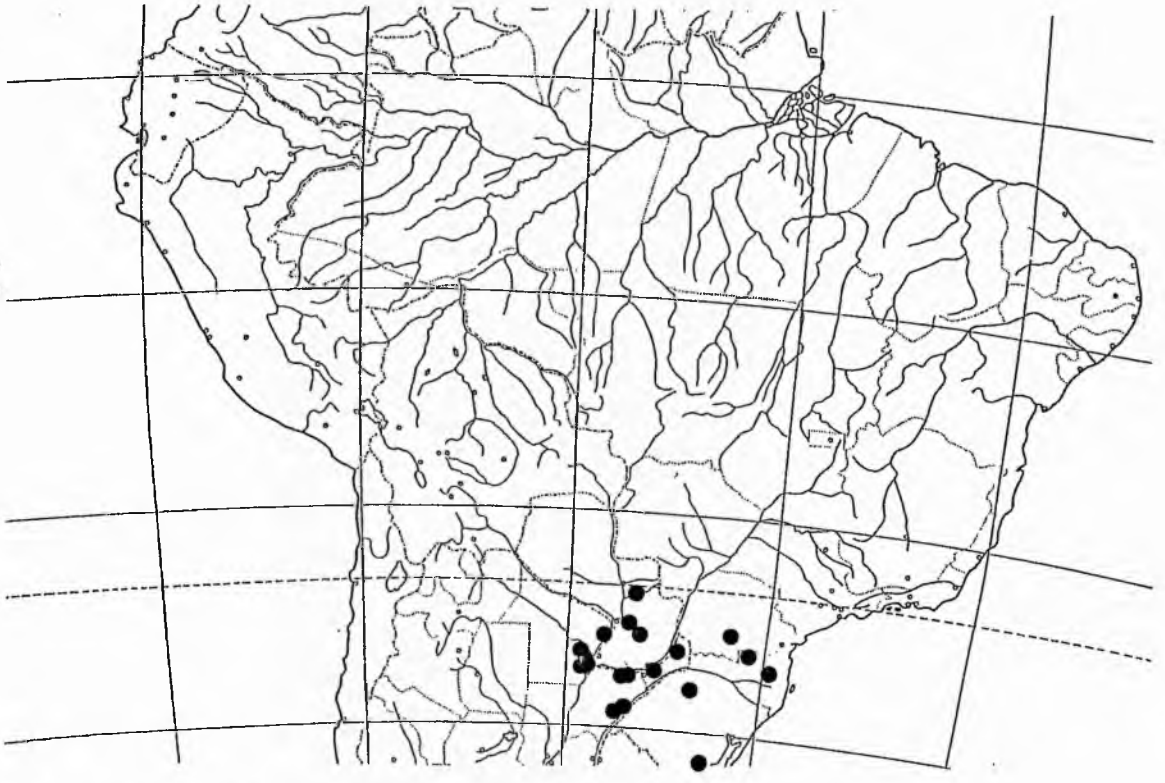
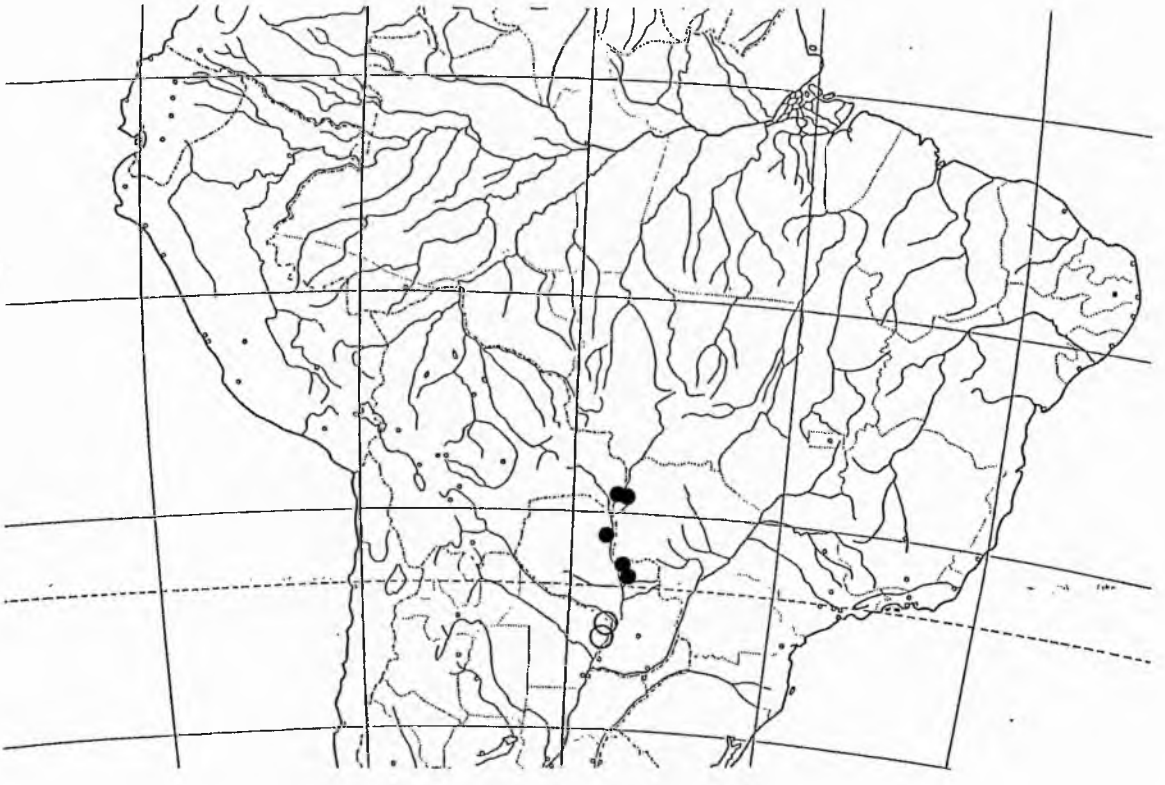


Fig. 5.89: Distribution map of *Maytenus ilicifolia*.

Fig. 5.90: Distribution map of *Ziziphus guaranitica*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.



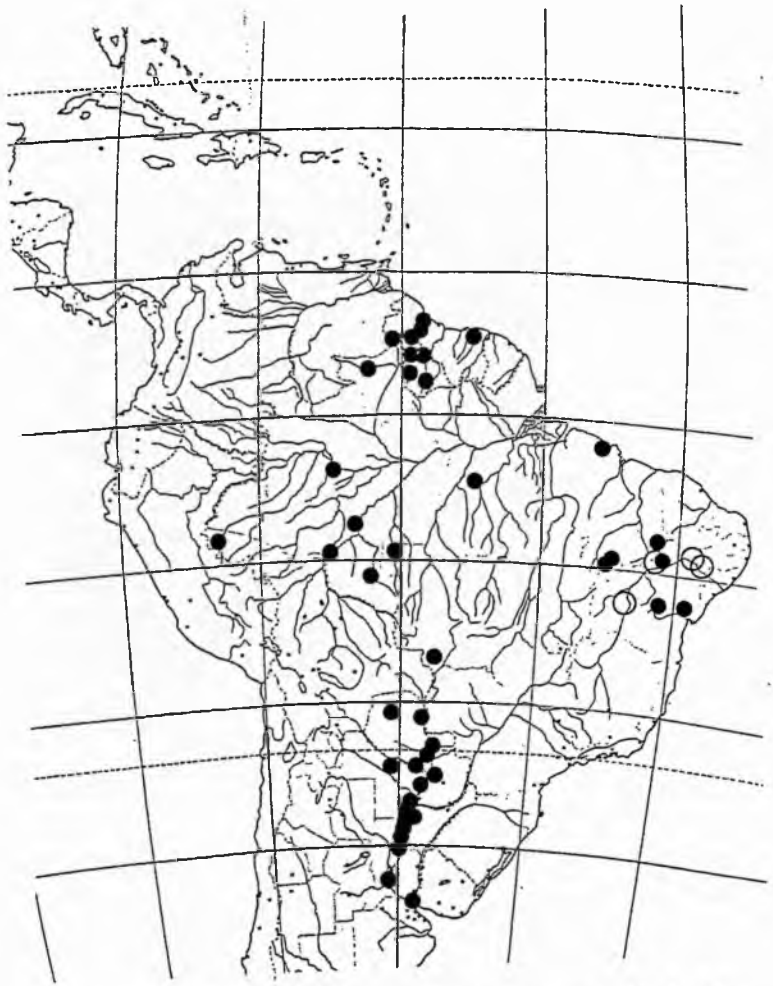


Fig. 5.91: Distribution map of *Albizia polyantha*. Solid black dots: herbarium exsiccata; open circles: citations in vegetation surveys.

Fig. 5.92: Distribution map of *Aspidosperma discolor*.

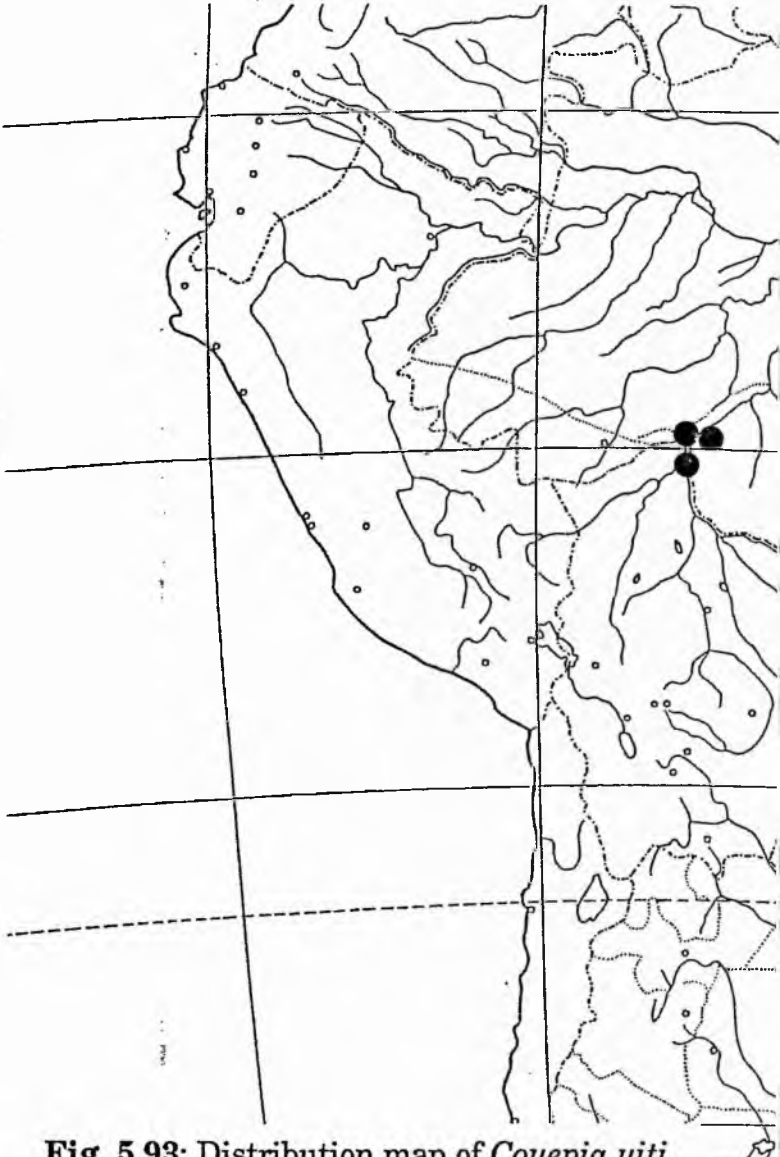
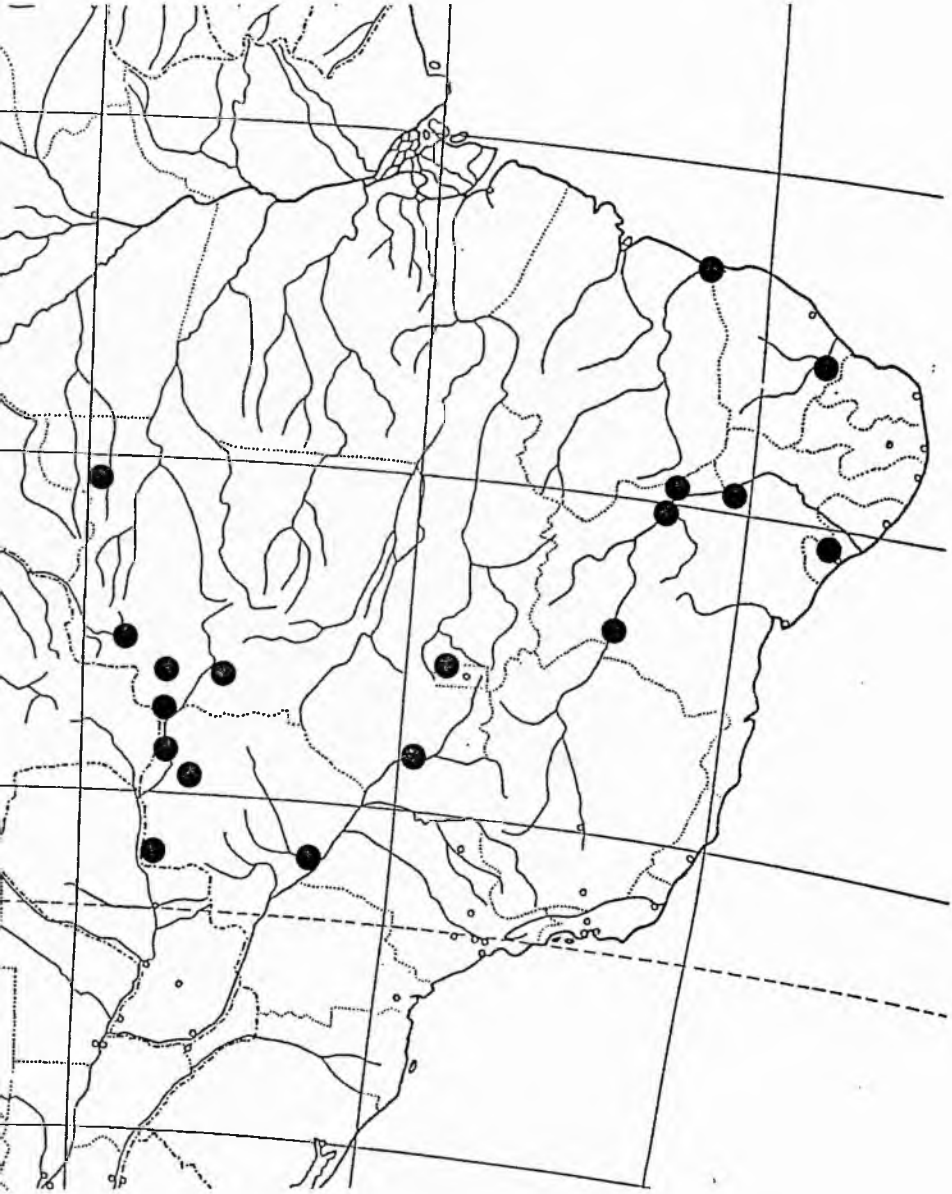


Fig. 5.93: Distribution map of *Couepia uiti*.



6. PHYTOSOCIOLOGICAL ANALYSIS OF NEOTROPICAL SEASONAL FORESTS

In order to assess to what an extent the Neotropical seasonal forests are interrelated and/or to other South American formations, reliable floristic lists were selected from the available literature and worked out in phytosociological tables on a basis of presence-absence of species. These data were then analyzed following three different techniques:

a) Classic phytosociological analysis of the Zürich-Montpellier school, in the more modern version modified by Mueller-Dombois & Ellenberg (1974). This consists essentially in listing all the species (rows) occurring in certain areas or localities (columns), and then mechanically search for species with common patterns of distribution in the columns. Subsequent reshuffling of columns and rows generally results in the grouping of some species which seem to be exclusive to a determined group of localities, exclusive to a single area, or common to most or all of them. These species groups are taken to indicate the presence of common environmental factors by which they are restricted in their phytogeographical distribution. Therefore, such groups have an ecological indicator value, and they are referred to as 'floristic groups (FG)' (Mueller-Dombois & Ellenberg, 1974). Because of the subjective nature of this analysis it is necessary to compare the results with those of more objective statistical studies, as the following.

b) Multivariate numerical methods:

b.1- CLINK (Complete Linkage) algorithm from Wishart's (1987) package, employing Sørensen's (1948) similarity index (also known as Czekanowski-Dice coefficient). This agglomerative technique of classification fuses the individuals (localities/areas) into increasingly larger discrete groups, based on their similarity matrix, and a dendrogram is provided to show their relationships. The fusion is interrupted according to a subjective criterion, generally when recognizable clusters of ecologically-floristically related individuals are formed, or when no individual is left isolated (Mateucci & Colma, 1982).

b.2- PCA (Principal Components Analysis) from the JMP IN™ statistical software. This ordination technique, contrary to the classificatory ones, does not establish discrete classes but displays the individuals under study in a hyper-dimensional space along axes of continuous variation.

The axes ('principal components') are numbered according to the decreasing percentage of accumulated variation they concentrate. Thus, Axis I always comprises the highest value of variation absorbed by any possible axis, which can then be interpreted as representing one particular environmental or ecological factor. The individuals are then displayed in succesive two-dimensional plots ('scattergrams'), of which only the Axis I-Axis II coordinates are shown and discussed here.

6.1- The woody Chaco communities and neighbouring formations:

All the vegetation types described in Chapter 2 and usually regarded as part of the Gran Chaco region have been analyzed in Table 6.1. A number of FG, namely II, V, VI and XII amongst others, indicate very close links between those woody communities of wetter and less frost-affected areas, such as **A** (Gallery Forest), **B** ('Selva de Ribera'), **C** ('Tipa-Pacará' Forest), **D** ('Palo blanco' Forest) and the Austro-Brazilian Transitional Forest (**E**), alongside the communities described by Prado et al. (in press, b) for Mato Grosso do Sul (**F**, **G**, **H**, **I** and **J**). Apart from FG XXI, which comprises species with a wide ecological plasticity, there are scarce connections between communities **A** to **J** and what is here regarded as Chaco *s.s.* (communities **K** to **W**). The FG XXII comprises the species that relate the Austro-Brazilian Transitional Forest to the Chaco proper, which are on the one hand of scarce importance here and sometimes accidental, and on the other are overweighed by the much more relevant links to communities **A** to **D**. The Chaco forest of Porto Murtinho (**J**) is the only one between the communities of Mato Grosso do Sul that can be regarded as truly chaquenian, as shown by Table 6.1 and coinciding with Prado et al. (in press, b). The FG XXIII, XXIV, XXV, XXVI, XXVII, XXVIII, XXXIII and XXXIV illustrate the strong internal homogeneity of the Chaco *s.s.* woody communities.

Figure 6.1 shows the dendrogram resulting from the CLINK classification analysis applied to the same set of communities shown in Table 6.1. It is noteworthy that the order of the communities rendered by CLINK is basically very similar to that proposed in the phytosociological table, save for the position of the Chaco at Porto Murtinho. Group α comprises communities **A** to **E**, while β those of Mato Grosso do Sul (**F** to **I**). Meanwhile, groups γ and δ consist of all the communities of the

TABLE 6.1: **Phytosociological analysis of the main woody communities of the Chaco and neighbouring formations.**

Column **A**: Gallery Forest, Paraná River (Franceschi & Lewis, 1979)

B: 'Selva de Ribera' (Prado et al., in press a; Morello & Adám., 1974)

C: 'Tipa-Pacará' Forest (Meyer, 1963; Digilio & Legname, 1966; Brown et al., 1985)

D: 'Palo blanco' Forest (Meyer, 1944; Coro, 1956; Adámoli et al., 1972; Cabrera, 1976)

E: Austro-Brazilian Transitional Forest (Lewis & Pire, 1981, and author's field experience; also Morello et al.,1971, Morello & Adámoli, 1974, and Cabrera, 1976)

F: Calcareous woodlands, M. Grosso do Sul (Prado et al., in press b)

G: *Schinopsis balansae* parkland, M.G. Sul (Prado et al., in press b)

H: *Aspidosperma-Mimosa* scrubland, M. Gr. do Sul (Prado et al., in press b)

I: *Diplokeleba-Tabebuia-Capparis* scrubland, M. Gr. do Sul (Prado et al., in press b)

J: Chaco forest, Pto Murtinho, M. Grosso do Sul (Prado et al., in press b)

K: 'Quebrachal' of *Schinopsis balansae* (Lewis & Pire, 1981, and author's field experience)

L: 'Quebrachal' of 3 'quebrachos' (Ragonese, 1941; Lewis & Pire, 1981, and author's field experience)

M: 'Quebrachal' of 2 'quebrachos' (Morello & Adámoli, 1968; Adámoli et al., 1972, and author's field experience)

N: 'Quebrachal' of white 'quebracho' (Morello et al., 1971; Lewis & Pire, 1981)

O: 'Palosantal' of *Bulnesia sarmientoi* (Morello et al., 1971, and Adámoli et al., 1972)

P: 'Algarrobal' of *Prosopis* spp. (Morello et al., 1971)

Q: 'Vinalar' of *Prosopis ruscifolia* (Morello et al., 1971)

R:'Palmar' of *Copernicia australis* , Western Chaco (Cabrera, 1976)

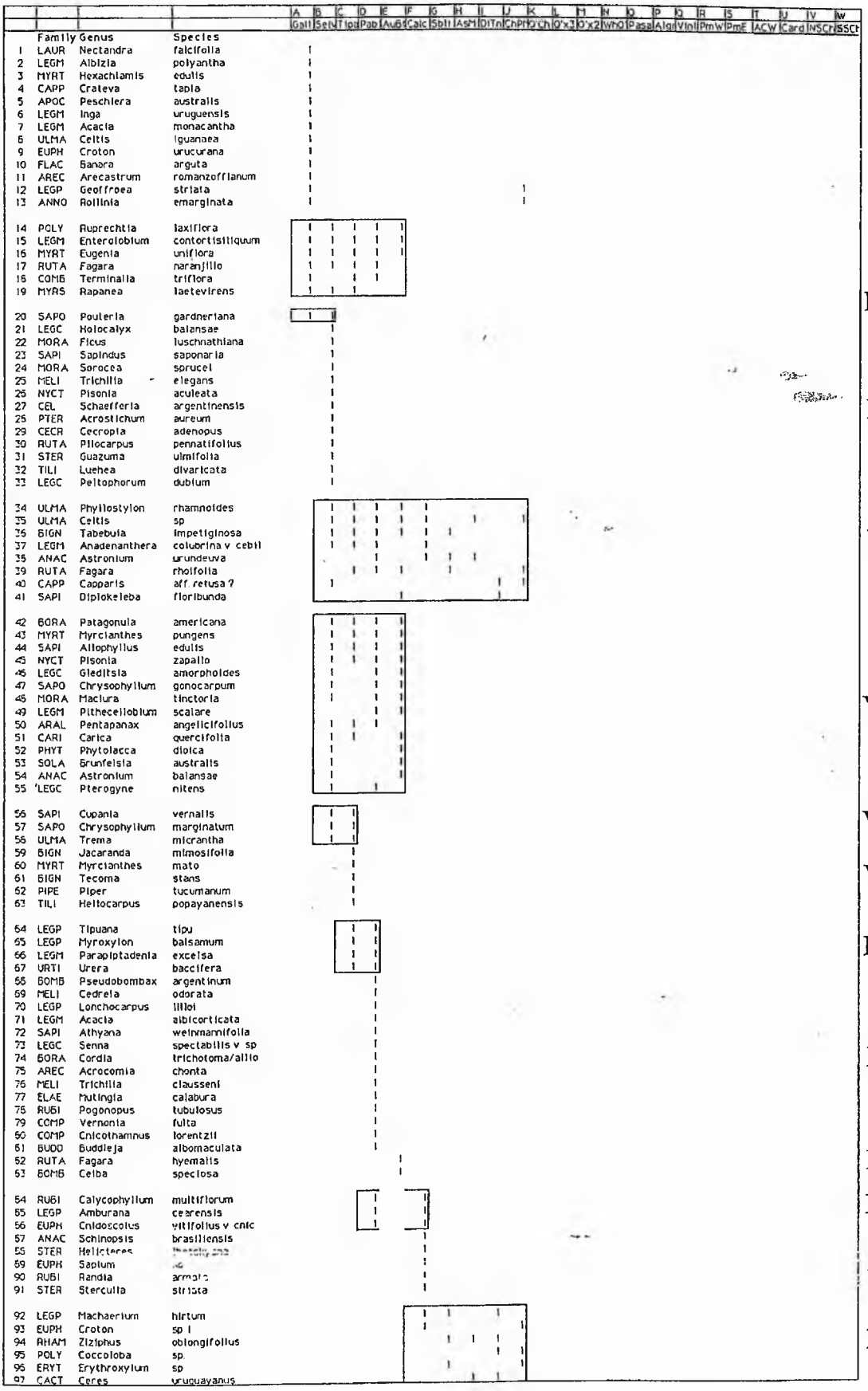
S: 'Palmar' of *Copernicia australis* , Eastern Chaco (Cabrera, 1976; Lewis & Pire, 1981, and author's field experience)

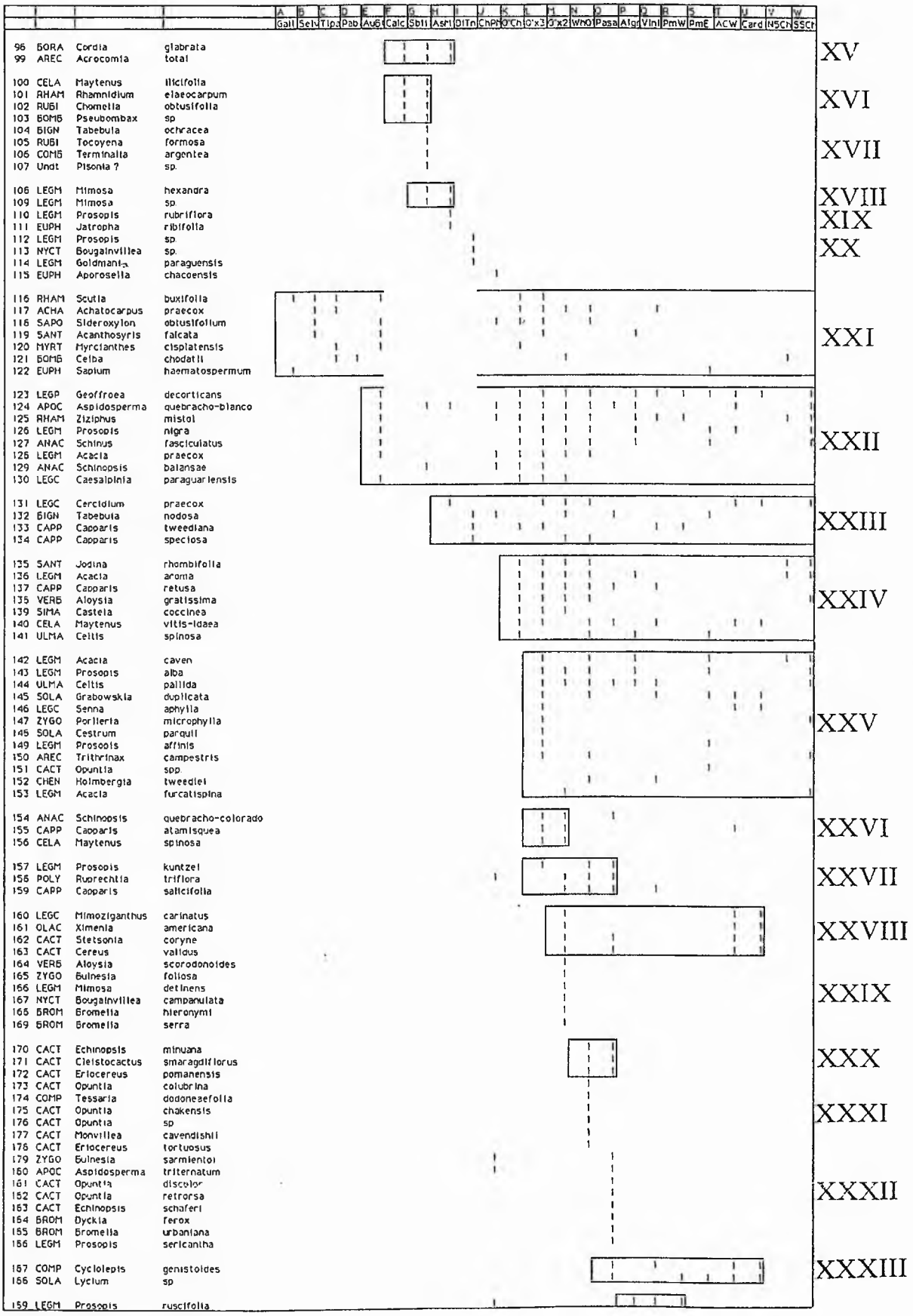
T: Arid Chaco Woodland (Sayago, 1969)

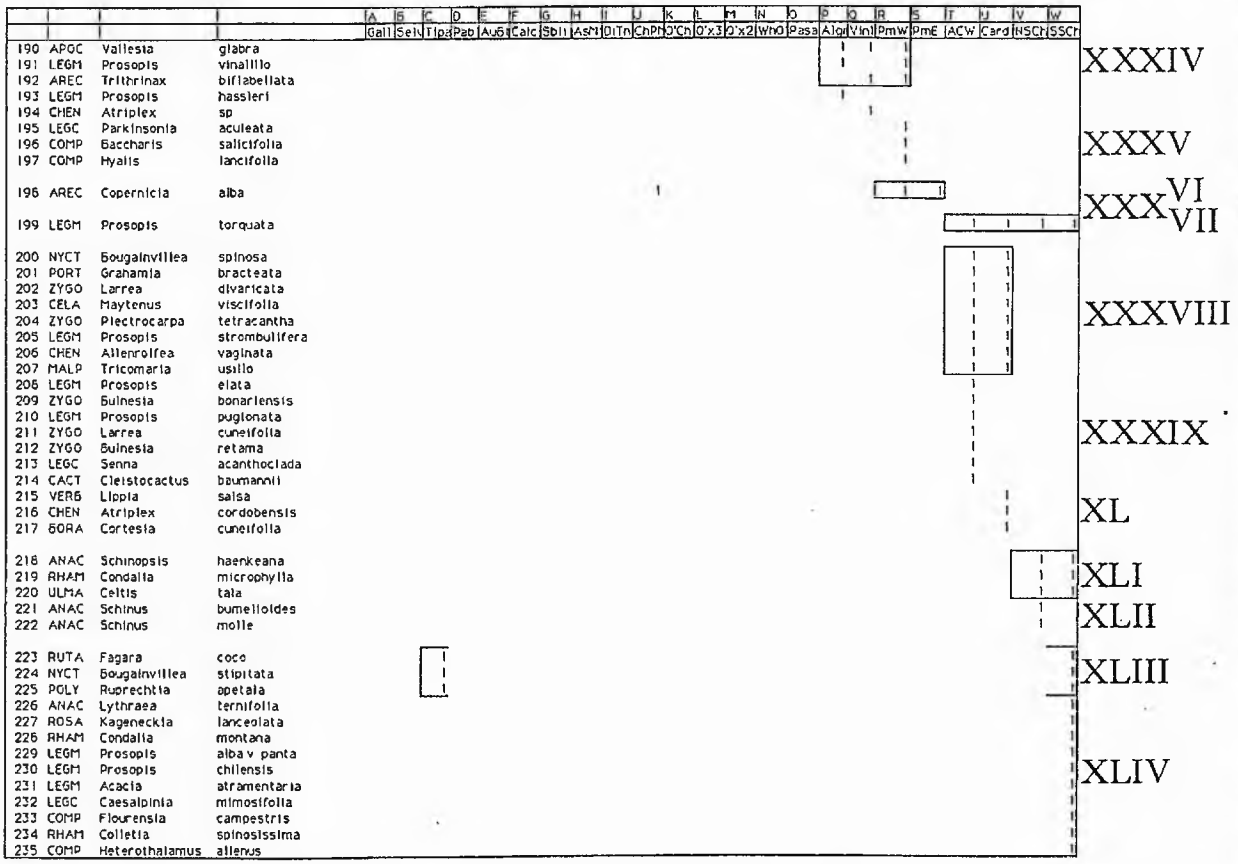
U: 'Cardonal' of *Stetsonia coryne* (Sayago, 1969)

V: North Sierra Chaco (Marlange, 1972)

W: South Sierra Chaco (Sayago, 1969)


A Gall
B SeNT
C Ipa
D Pab
E Au6
F Calc
G Sbti
H AsM
I DiTn
J ChPrh
K ch,l0'x3
L 0'x2
M whO
N Pasa
O Alga
P Vinli
Q PmW
R PmE
S ACW
T Card
U INSCh
V SSCh
W
Family Genus Species
1 LAUR Nectandra falcifolia
2 LEGM Albizia polyantha
3 MYRT Hexachlamis edulis
4 CAPP Crateva tapia
5 APOC Peschiera australis
6 LEGM Inga uruguensis
7 LEGM Acacia monacantha
8 ULMA Celtis iguanaea
9 EUPH Croton urucurana
10 FLAC Banara arguta
11 AREC Arecastrum romanzoffianum
12 LEGP Geoffroea striata
13 ANNO Rollinia emarginata
14 POLY Ruprechtia laxiflora
15 LEGM Enterolobium contortisiliquum
16 MYRT Eugenia uniflora
17 RUTA Fagara naranjillo
18 COMB Terminalia triflora
19 MYRS Rapanea laetevirens
20 SAPO Pouteria gardneriana
21 LEGC Holocalyx balansae
22 MORA Ficus luschnathiana
23 SAPI Sapindus saponaria
24 MORA Sorocea sprucei
25 MELI Trichilia elegans
26 NYCT Pisonia aculeata
27 CEL Schaefferia argentinensis
28 PTER Acrostichum aureum
29 CECR Cecropia adenopus
30 RUTA Pilocarpus pennatifolius
31 STER Guazuma ulmifolia
32 TILI Luehea divaricata
33 LEGC Peltophorum dubium
34 ULMA Phyllostylon rhamnoides
35 ULMA Celtis sp
36 BIGN Tabebuia impetiginosa
37 LEGM Anadenanthera colubrina v cebil
38 ANAC Astronium urundeuva
39 RUTA Fagara rhoifolia
40 CAPP Capparis aff. retusa ?
41 SAPI Diplokeleba floribunda
42 BORA Patagonula americana
43 MYRT Myrcianthes pungens
44 SAPI Allophylus edulis
45 NYCT Pisonia zapallo
46 LEGC Gleditsia amorphoides
47 SAPO Chrysophyllum gonocarpum
48 MORA Maclura tinctoria
49 LEGM Pithecellobium scalare
50 ARAL Pentapanax angelicifolius
51 CARI Carica quercifolia
52 PHYT Phytolacca dioica
53 SOLA Brunfelsia australis
54 ANAC Astronium balansae
55 LEGC Pterogyne nitens
56 SAPI Cupania vernalis
57 SAPO Chrysophyllum marginatum
58 ULMA Trema micrantha
59 BIGN Jacaranda mimosifolia
60 MYRT Myrcianthes mato
61 BIGN Tecoma stans
62 PIPE Piper tucumanum
63 TILI Heliocarpus popayanensis
64 LEGP Tipuana tipu
65 LEGP Myroxylon balsamum
66 LEGM Parapiptadenia excelsa
67 URTI Urera baccifera
68 BOMB Pseudobombax argentinum
69 MELI Cedrela odorata
70 LEGP Lonchocarpus lilloi
71 LEGM Acacia albicorticata
72 SAPI Athyana weinmannifolia
73 LEGC Senna spectabilis v sp
74 BORA Cordia trichotoma/allio
75 AREC Acrocomia chonta
76 MELI Trichilia claussenii
77 ELAE Mutingia calabura
78 RUBI Pogonopus tubulosus
79 COMP Vernonia fulta
80 COMP Cnicothamnus lorentzii
81 BUDD Buddleja albomaculata
82 RUTA Fagara hyemalis
83 BOMB Ceiba speciosa
84 RUBI Calycophyllum multiflorum
85 LEGP Amburana cearensis
86 EUPH Cnidoscolus vitifolius v cnic
87 ANAC Schinopsis brasiliensis
88 STER Helicteres
89 EUPH Sapium
90 RUBI Randia armata
91 STER Sterculia striata
92 LEGP Machaerium hirtum
93 EUPH Croton sp 1
94 RHAM Ziziphus oblongifolius
95 POLY Coccoloba sp.
96 ERYT Erythroxylum sp
97 CACT Ceres uruguayanus
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV


A Gait
B Sel
E Tip
D Pab
E Au6
F Calc
G Sb11
H Asm
I DITn
J ChP
K ChO
L ChO x3
M ChO x2
N Wh01
O Posa
P Algg
Q Vin
R PmW
S PmE
T ACW
U Card
V N5Cn
W S5Ch
96 BORA Cordia glabrata
99 AREC Acrocomia total
XV
100 CELA Maytenus ilicifolia
101 RHAM Rhamnidium elaeocarpum
102 RUBI Chomelia obtusifolia
XVI
103 BOMB Pseudobombax sp
104 BIGN Tabebuia ochracea
105 RUBI Tocoyena formosa
106 COMB Terminalia argentea
107 Undt Piscnia ?
sp.
XVII
108 LEGM Mimosa hexandra
109 LEGM Mimosa sp.
XVIII
110 LEGM Prosopis rubriflora
111 EUPH Jatropha ribifolia
XIX
112 LEGM Prosopis sp.
113 NYCT Bougainvillea sp.
XX
114 LEGM Goldmania paraguensis
115 EUPH Aporosella chacoensis
116 RHAM Scutia buxifolia
117 ACHA Achatocarpus praecox
118 SAPO Sideroxylon obtusifolium
119 SANT Acanthosyris falcata
120 MYRT Myrcianthes cisplatensis
121 BOMB Ceiba chodatii
122 EUPH Sapium haematospermum
XXI
123 LEGP Geoffroea decorticans
124 APOC Aspidosperma quebracho-blanco
125 RHAM Ziziphus mistol
126 LEGM Prosopis nigra
127 ANAC Schinus fasciculatus
128 LEGM Acacia praecox
129 ANAC Schinopsis balansae
130 LEGC Caesalpinia paraguariensis
XXII
131 LEGC Cercidium praecox
132 BIGN Tabebuia nodosa
133 CAPP Capparis tweediana
134 CAPP Capparis speciosa
XXIII
135 SANT Jodina rhombifolia
136 LEGM Acacia aroma
137 CAPP Capparis retusa
138 VERB Aloysia gratissima
139 SIMA Castela coccinea
140 CELA Maytenus vitis-idaea
141 ULMA Celtis spinosa
XXIV
142 LEGM Acacia caven
143 LEGM Prosopis alba
144 ULMA Celtis pallida
145 SOLA Grabowskia duplicata
146 LEGC Senna aphylla
147 ZYGO Porlieria microphylla
148 SOLA Cestrum parquii
149 LEGM Prosopis affinis
150 AREC Trithrinax campestris
151 CACT Opuntia spp.
152 CHEN Holmbergia tweediei
153 LEGM Acacia furcatispina
XXV
154 ANAC Schinopsis quebracho-colorado
155 CAPP Capparis atamisquea
156 CELA Maytenus spinosa
XXVI
157 LEGM Prosopis kuntzei
158 POLY Ruprechtia triflora
159 CAPP Capparis salicifolia
XXVII
160 LEGC Mimoziganthus carinatus
161 OLAC Ximenia americana
162 CACT Stetsonia coryne
163 CACT Cereus validus
164 VERB Aloysia scorodonoides
165 ZYGO Bulnesia foliosa
166 LEGM Mimosa detinens
167 NYCT Bougainvillea campanulata
168 BROM Bromelia hieronymi
169 BROM Bromelia serra
XXVIII
XXIX
170 CACT Echinopsis minuana
171 CACT Cleistocactus smaragdiflorus
172 CACT Eriocereus pomanensis
173 CACT Opuntia colubrina
174 COMP Tessaria dodoneaefolia
175 CACT Opuntia chakensis
176 CACT Opuntia sp
177 CACT Monvillea cavendishii
178 CACT Eriocereus tortuosus
XXX
XXXI
179 ZYGO Bulnesia sarmientoi
180 APOC Aspidosperma triternatum
181 CACT Opuntia discolor
182 CACT Opuntia retrorsa
183 CACT Echinopsis schaferi
184 BROM Dyckia ferox
185 BROM Bromelia urbaniana
186 LEGM Prosopis sericantha
XXXII
187 COMP Cyclolepis genistoides
188 SOLA Lycium sp
XXXIII
189 LEGM Prosopis ruscifolia


A Gall
B Sel
C Tipa
D Pab
E Aug
F Calc
G Sb11
H As*1
I DiTn
J ChPN
K 0'Ch
L 0'x3
M 0'x2
N WhO
O Pasa
P Alor
Q Vin
R PmW
S PmE
T ACW
U Card
V NSCh
W SSCh
190 APOC Vallesia glabra
191 LEGM Prosopis vinalillo
192 AREC Trithrinax biflabellata
193 LEGM Prosopis hassleri
194 CHEN Atriplex sp
195 LEGC Parkinsonia aculeata
196 COMP Baccharis salicifolia
197 COMP Hyalis lancifolia
198 AREC Copernicia alba
199 LEGM Prosopis torquata
200 NYCT Bougainvillea spinosa
201 PORT Grahamia bracteata
202 ZYGO Larrea divaricata
203 CELA Maytenus viscifolia
204 ZYGO Plectrocarpa tetracantha
205 LEGM Prosopis strombulifera
206 CHEN Allenrolfea vaginata
207 MALP Tricomaria usillo
208 LEGM Prosopis elata
209 ZYGO Bulnesia bonariensis
210 LEGM Prosopis pugionata
211 ZYGO Larrea cuneifolia
212 ZYGO Bulnesia retama
213 LEGC Senna acanthoclada
214 CACT Cleistocactus baumannii
215 VERB Lippia salsa
216 CHEN Atriplex cordobensis
217 BORA Cortesia cuneifolia
218 ANAC Schinopsis haenkeana
219 RHAM Condalia microphylla
220 ULMA Celtis tala
221 ANAC Schinus bumelioides
222 ANAC Schinus molle
223 RUTA Fagara coco
224 NYCT Bougainvillea stipitata
225 POLY Ruprechtia apetala
226 ANAC Lythraea ternifolia
227 ROSA Kageneckia lanceolata
228 RHAM Condalia montana
229 LEGM Prosopis alba v panta
230 LEGM Prosopis chilensis
231 LEGM Acacia atramentaria
232 LEGC Caesalpinia mimosifolia
233 COMP Flourensia campestris
234 RHAM Colletia spinosissima
235 COMP Heterothalamus alienus
XXXIV
XXXV
XXXVI
XXXVII
XXXVIII
XXXIX
XL
XLI
XLII
XLIII
XLIV

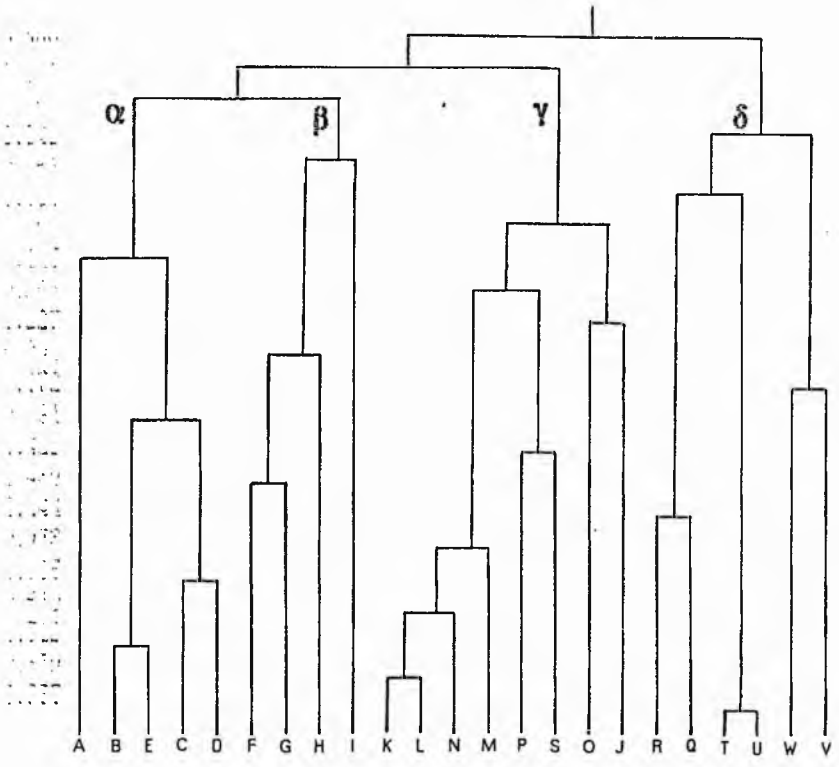


Fig. 6.1: Dendrogram resulting from CLINK classification analysis of the main woody communities of the Chaco and neighbouring formations. Letters in the bottom line indicate the communities studied (see Table 6.1 for key), and the figures in the vertical line the similarity index value at each level of fusion.

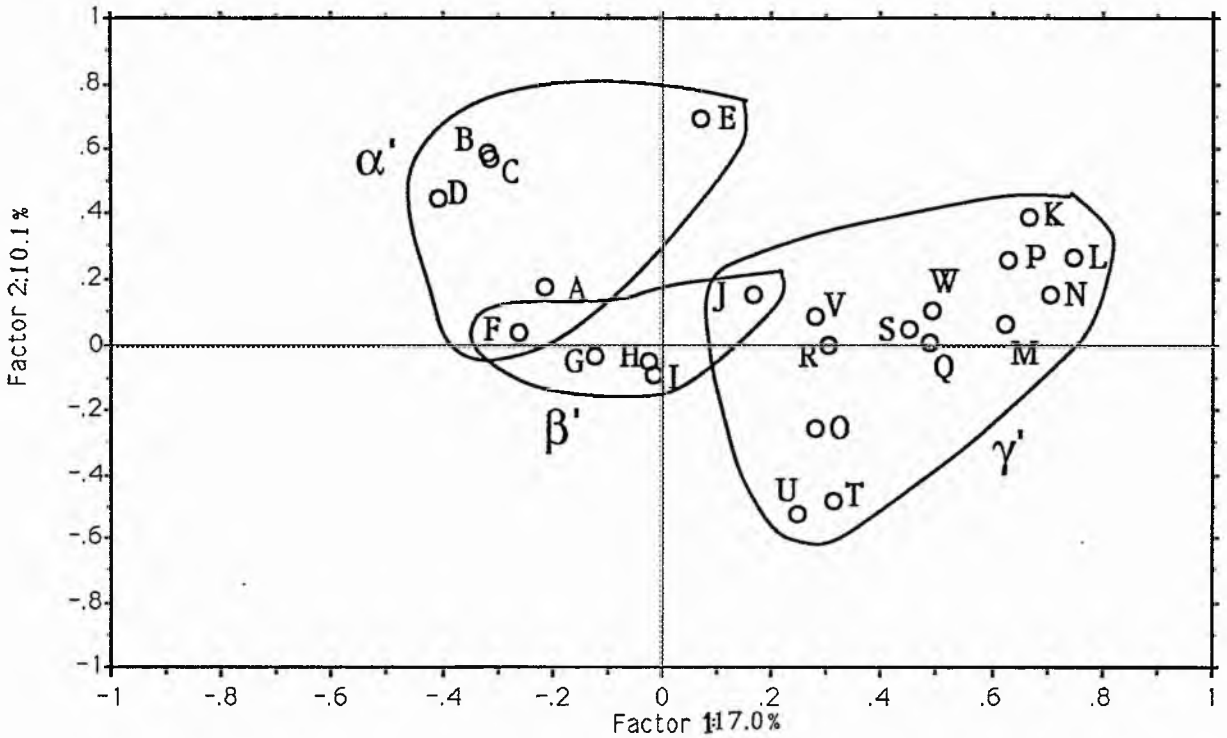


Fig. 6.2: Scattergram from PCA analysis of the main woody communities of the Chaco and neighbouring formations. See explanation in text.

Chaco *s.s.*, separated into two groups probably because of an east-west floristic gradient within the province.

The results of the PCA analysis shown in Fig. 6.2 present three basic clusterings of communities: the wetter ones (**A** to **F**) are together in cluster α', the Mato Grosso do Sul communities are grouped in another one (β'), while the bulk of the Chaco s.s. in cluster γ' shows stronger links within itself than with the rest of the neighbouring formations. Once again the Chaco of Porto Murtinho is in a transitional position and could pertain to either of two clusters, while the Austro-Brazilian Transitional Forest (**E**) unmistakably joins the group of wetter communities.

6.2- South American Seasonal Forests: a global comparison.

The vegetation units involved in this comparative study are:

Chaquenian Dominium

A- The Monte province (*sensu* Morello, 1958).

B- The Chaco province: the Sierra Chaco is placed here in a separate column to test the consistency of the inclusion of this district within the Chaco *s.s.*.

C- The Chaco province: the lowland Chaco in its Eastern, Central and Western districts. Floristic list taken from Sect. 4.1, excluded those species exclusive to the Sierra Chaco.

Neotropical Seasonal Forests of South America

D- Austro-Brazilian Transitional Forest, as defined and described in Sect. 2.3.3.a; the results of this analysis will further allow to discuss its present position within the Chaco province.

E- 'Selva de Ribera', on the levee limiting the river Paraná flooding valley, as described in Sect. 2.3.2 and in Prado et al. (in press, a). It is not yet clear if previous phytogeographical accounts have placed this community in the Chaco or other province, basically because it has been ignored as a vegetation unit by most authors, but the present author believes it should be regarded as part of the Paranense province *sensu* Cabrera & Willink (1980).

F- Gallery Forest in the Paraná river valley, as part of the Paranense province (Cabrera, 1976).

G- Upper Uruguay River Valley Forests, part of the Paranense province *sensu* Cabrera & Willink (1980).

H- Planalto Forest in São Paulo state, part of the Paranense province *sensu* Cabrera & Willink (1980).

I- Subandean Piedmont Forests, in both its 'Palo blanco' and 'Tipa-Pacará' variants. Floristic list taken from Sect. 4.3. At present a member of the Yungas province (Cabrera, 1976), but repeatedly regarded as chaquenian by previous authors.

J- The Caatingas province, until present regarded as a member of the Chaquenian Dominium by Cabrera & Willink (1980). Floristic list taken from Sect. 4.2.

K- Calcareous forests of Mato Grosso do Sul, of uncertain phytogeographical position so far.

L- The calcareous forest of Januária area, very close geographically and floristically to the Caatingas (Ratter et al., 1978; Andrade-Lima, 1981).

M- The dry Caribbean vegetation of Venezuela. The floristic list is an aggregate, ranging from Aristeguieta's (1968) "selva veranera" (summer-green forest) to semiarid scrublands (Matteucci & Colma, 1982). It corresponds to the Guajira province in the Caribbean Dominium (Cabrera & Willink, 1980).

N- Equivalent communities in dry Caribbean Colombia, also part of the Guajira province.

O- Dry forests, woodlands and savannas of W Ecuador, as in Acosta-Solís (1966) and Harling (1979). At present in the Pacific province of the Amazonian Dominium (Cabrera & Willink, 1980).

Amazonian Dominium

Three floristic lists of localized vegetation areas corresponding to the three more conspicuous provinces of the Amazonian Dominium have been taken as paradigms.

P- A central area of the Brazilian Cerrados, in the Federal District (Ratter, 1986; P.E. Oliveira, pers. comm.).

Q- One stand of Atlantic rainforest in coastal São Paulo (Silva & Leitão Fº, 1982).

R- An area of Amazon forest close to Manaus (Prance et al., 1976).

Thus, the analysis performed on these data at both specific and generic level will allow one to establish how close the links Chaco-Caatingas are, vis-à-vis other similar kinds of vegetation in South America, and how well the Caatingas compare with the Chaquenian Dominium *versus* the Amazonian Dominium.

6.2.1- Analysis at specific level:

In Table 6.2 the results of the classic phytosociological approach at species level are shown. FG I assembles species of ample distribution in seasonal formations but absent from the more humid provinces (**P**, **Q** and **R**). FG II, III, IV and V indicate different degrees of relationship between the Chaco and also some of its neighbouring communities to the Subandean Piedmont Forests (**I**). FG VII comprises the rather weak links between the Chaquenian Dominium and the Guajira province and the dry forests in W Ecuador. FG VIII to XI show the consistency of the Chaco Dominium, clearly separating it from the rest of the formations included in this analysis.

The FG XII and XIII comprise those species generally restricted to the Pleistocenic Arc as here defined (see Sect. 5.3.1), although *Tabebuia impetiginosa* extends as far as Mexico. FG XIV and XV show the links between both the southern extensions of the Pleistocenic Arc, not including the Caatingas or related calcareous communities. FG XVI encompasses Caatingas species with a wide distribution in South America from the Pleistocenic Arc to Ecuador and the dry Caribbean area, whereas FG XVII is similar but it excludes the Caatingas. The FG XIX to XXVI show a number of floristic links of the Upper Uruguay Forests (**G**), out of which those with the Caatingas must be emphasized (FG XXI). Groups XXVII to XXX indicate varied connections of the Planalto Forest (**H**) of S Brazil. The FG XXXI, XXXII and XXXIII show the close contacts between the Subandean Piedmont Forests (**I**) to the Caatingas (**J**) and related calcareous communities (**K** and **L**, in turn connected to **J** by FG XXXIV to XXXVI). While the links Caatingas/Ecuador+dry Caribbean area are shown in FG XXXVII and XXXVIII, those of the same province with the Amazonian Dominium are evident in FG XXXIX and XL. The dry Caribbean sectors of Colombia and Venezuela are very closely related to each other (FG XLIII), while they show strong connections to the dry formations of W Ecuador (FG XLII and XLIV). FG XLV indicates some loose links of the Cerrados of central Brazil with a number of seasonal forests of South America.

The dendrogram rendered by the CLINK analysis is shown in Fig. 6.3, with four recognizable clusters and one isolated individual.

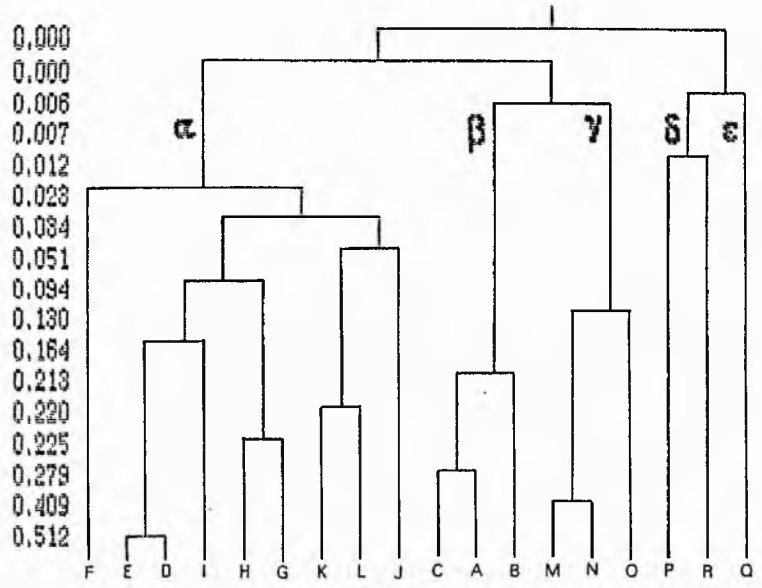


Fig. 6.3: Dendrogram resulting from CLINK classification analysis of the main South American seasonal forests, at specific level. Letters in the bottom line indicate the communities studied (see Table 6.2 for key), and the figures in the vertical line the similarity index value at each level of fusion.

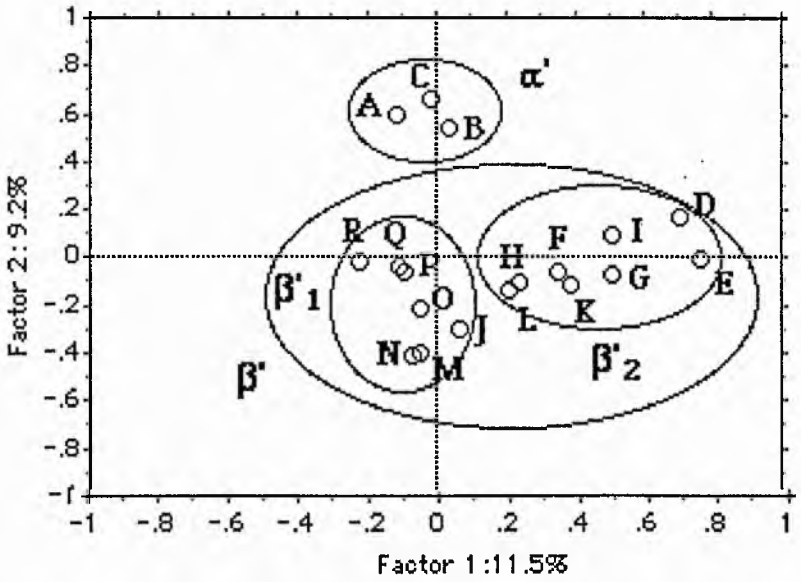


Fig. 6.4: Scattergram from PCA analysis of South American seasonal forests. See explanation in text.

Group α comprises two subclusters, one formed by the Caatingas (**J**) plus Calcareous forests and the other by the southernmost expansions of the Pleistocenic Arc, including both the Subandean Piedmont Forests (**I**) and the Austro-Brazilian Transitional Forest (**D**). Group β comprises the chaquenian vegetation types, whereas cluster γ comprises the vegetation of the dry Caribbean coast and W Ecuador. Finally, the Cerrados are closer to the Amazon forest stand (group δ), while the Atlantic rainforest remains isolated (ε).

The results of the PCA analysis are shown in Fig. 6.4. Clearly detached from all the rest of the vegetation types are the members of the Chaquenian Dominium (cluster α'). The remainder, although showing enough coherence to be regarded as a single cluster (β'), can be further separated in two subclusters. Subcluster β'_1 comprises the Caatingas and, closely related, the dry vegetation of Venezuela, Colombia and Ecuador, along with the three typical representatives of the Amazonian Dominium. Subcluster β'_2 consists of the southern half of the Pleistocenic Arc, including the Subandean Piedmont Forests (**I**) and the Austro-Brazilian Transitional Forest (**D**).

6.2.2- Analysis at generic level:

In Table 6.3 the results of the classic phytosociological study at generic level are shown. Once again the members of the Chaquenian Dominium (**A, B** & **C**) are well defined as a unit by the FG **VI, VII, VIII** and **IX**, while their links to the seasonal formations are illustrated by FG **X** to **XVI**. The genera restricted to the Pleistocenic Arc are between those in FG **XVIII** and **XXXVI**, whereas the genera which extend from the Pleistocenic Arc to the Guajira province and Ecuador are included in FG **XIX, XXIV, XXV, XXXIX** and **XL**. Some of the relevant genera of the Caatingas (**J**) and Subandean Piedmont Forests (**I**) are widespread in the Pleistocenic Arc but also occur in Colombia, Venezuela, Ecuador and the Amazonian Dominium (FG **XX, XXI** and **XXIX**). The generic links of the Upper Uruguay Forests (**G**) with the Caatingas (**J**) are shown in FG **XXVI**, while those with the Subandean Piedmont Forests (**I**) are indicated in FG **XXVII**. It is noteworthy that FG XXXVII emphasizes the floristic contacts at generic level of solely the Caatingas (**J**) and the Subandean Piedmont Forests (**I**), while FG **XLI** and **XLIII** those between the Caatingas and the Guajira province and W Ecuador(**M, N** and **O**). The

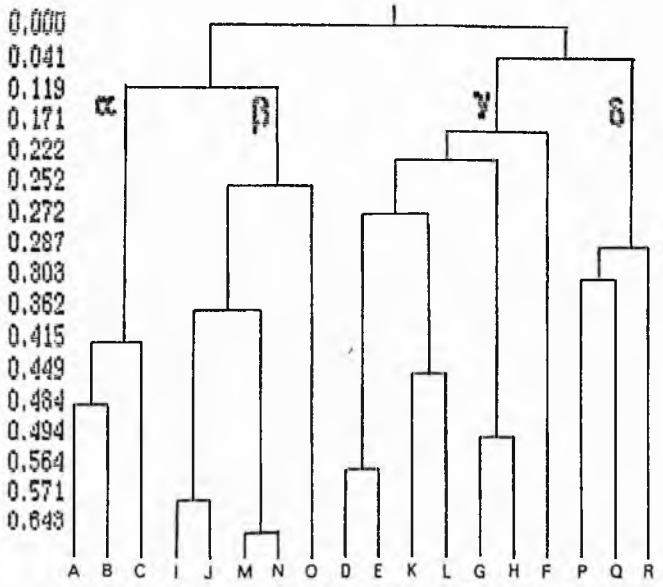


Fig. 6.5: Dendrogram resulting from CLINK classification analysis of the main South American seasonal forests, at generic level. Letters in the bottom line indicate the communities studied (see Table 6.2 for key), and the figures in the vertical line the similarity index value at each level of fusion.

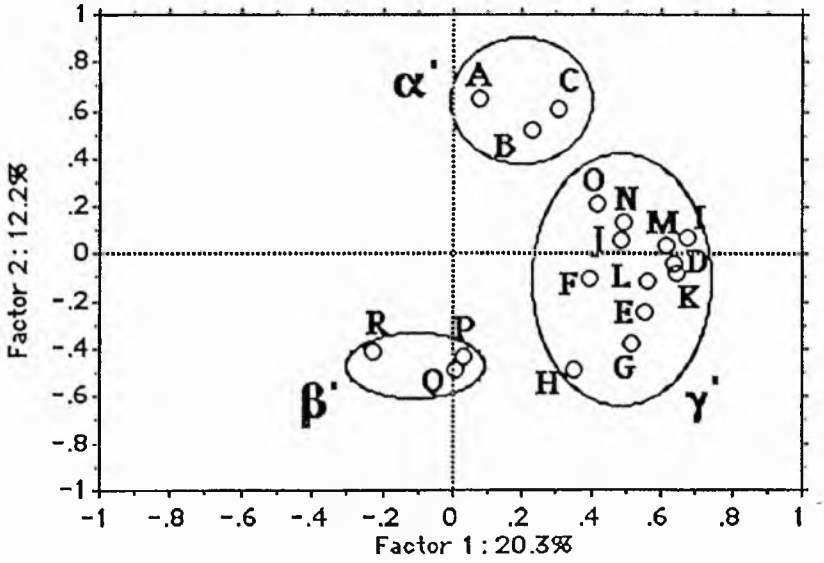


Fig. 6.6: Scattergram from PCA analysis of South American seasonal forests at generic level. See explanation in text.

floristic relationship Caatingas/Amazonian Dominium is shown in FG **XLIV** and **XLV**, while FG **L** to **LIII** indicate the internal coherence and close links between the formations of the Amazonian Dominium.

The dendrogram resulting from the CLINK analysis (Fig. 6.5) shows unmistakably that both the Chaquenian Dominium (group α) and Amazonian Dominium (group δ) are clearly isolated from the rest of the vegetation types. The group β emphasizes very close links at generic level between the Subandean Piedmont Forests, the Caatingas, the Guajira province and W Ecuador. Group γ comprises the Austro-Brazilian Transitional Forest together with the rest of the southern seasonal forests.

The previous results are remarkably congruent with the scattergram of Fig. 6.6, where again the Chaquenian (cluster α') and Amazonian (cluster β') dominia are plainly detached from the seasonal forests, which in this case are together in a single cluster (γ'). The latter shows anyhow that the Caatingas (**J**) are floristically very close to the Guajira province (**M** and **N**), W Ecuador (**O**) and the Subandean Piedmont Forests (**I**).

TABLE 6.2: **Phytosociological analysis of the main South American Seasonal Forests. Specific level.**

Column **A**- The Monte province, Argentina (*sensu* Morello, 1958:145-50).

B- Chaco *s.s.*: Sierra Chaco, Argentina (Sayago, 1969, p.224).

C- Chaco *s.s.*: the lowland Chaco in its Eastern, Central and Western districts, Argentina. Floristic list from Sect. 4.1, excluded the species exclusive to the Sierra Chaco.

D- Austro-Brazilian Transitional Forest, Argentina (see Sect. 2.3.3.a). Floristic list from Lewis & Pire, 1981, and author's field experience; also Morello et al.,1971, Morello & Adámoli, 1974, and Cabrera, 1976.

E- 'Selva de Ribera', Argentina (Prado et al., in press a; Morello & Adámoli, 1974).

F- Gallery Forest, Argentina (Franceschi & Lewis, 1979).

G- Upper Uruguay River Valley Forests, Santa Catarina and Rio Grande do Sul, Brazil (Klein, 1972; Rambo, 1980).

H- Planalto Forest, Vassununga & Bauru, São Paulo, Brazil (Martins, 1979, pp 108-9; Cavassan et al., 1984).

I- Subandean Piedmont Forests, in both its 'Palo blanco' and 'Tipa-Pacará' variants. Floristic list taken from Sect. 4.3.

J- The Caatingas province, Brazil. Floristic list: Sect. 4.2.

K- Calcareous woodlands, Mato Grosso do Sul, Brazil (Ratter et al., 1988b, p.516; Prado et al., in press b).

L- Calcareous forest, Januária, MG, Brazil (Ratter et al., 1978).

M- Dry Caribbean vegetation of Venezuela. The floristic list is an aggregate of Aristeguieta's (1968) "selva veranera" (summer-green forest) and semiarid scrublands (Matteucci & Colma, 1982, pp 102-4).

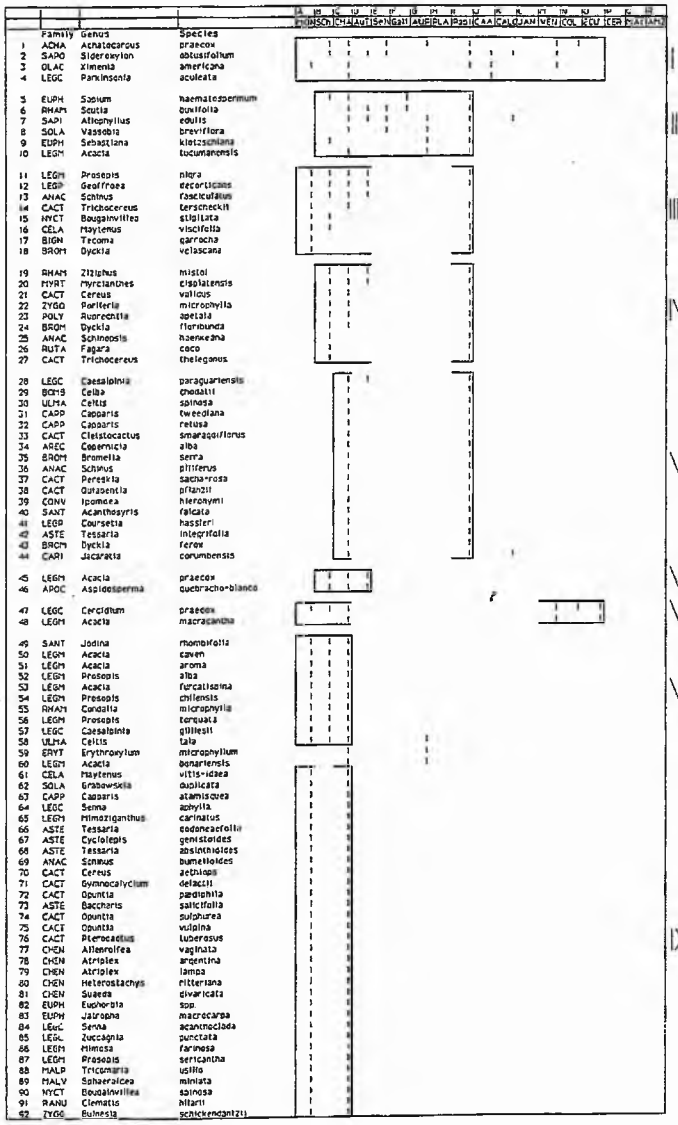
N- Dry Caribbean vegetation of Colombia (Dugand, 1970, pp 428-31; Rieger, 1976, pp 40-1).

O- Dry forests, woodlands and savannas of W Ecuador, as in Acosta-Solís (1966, pp 413-5) and Harling (1979).

P- Cerrado and cerradão in Brasília, Federal District (Ratter, 1986; P.E. Oliveira, pers. comm.).

Q- Atlantic rainforest , Ubatuba, SP, Brazil (Silva & Leitão Fº, 1982).

R- Amazon forest, km 30 on the road Manaus-Itacoatiara, Amazonas, Brazil (Prance et al., 1976,pp 28-35).


Family Genus Species
1 ACHA Achatocarpus praecox
2 SAPO Sideroxylon obtusifolium
3 OLAC Ximenia americana
4 LEGC Parkinsonia aculeata
5 EUPH Sebastiana haematospermum
6 RHAM Scutia buxifolia
7 SAPI Allophyllus edulis
8 SOLA Vassobia brevriflora
9 EUPH Sebastiana klotzschiana
10 LEGM Acacia tucumanensis
11 LEGM Prosopis nigra
12 LEGP Geoffroea decorticans
13 ANAC Schinus rasekuifolius
14 CACT Trichocereus terscheckii
15 NYCT Bougainvillea stipitata
16 CELA Maytenus viscifolia
17 BIGN Tecoma garrocha
18 BROM Dyckia velascana
19 RHAM Ziziphus mistol
20 MYRT Myrcianthes cisplatensis
21 CACT Cereus validus
22 ZYGO Porlieria microphylla
23 POLY Ruprechtia apetala
24 BROM Dyckia floribunda
25 ANAC Schinopsis haenkeana
26 RUTA Fagara coco
27 CACT Trichocereus thelegonus
28 LEGC Caesalpinia paraguariensis
29 BOMB Ceiba chodatii
30 ULMA Celtis spinosa
31 CAPP Capparis tweediana
32 CAPP Capparis retusa
33 CACT Cleistocactus smaragdiflorus
34 AREC Copernicia alba
35 BROM Bromelia serra
36 ANAC Schinus pilifierus
37 CACT Pereskia sacharosa
38 CACT Quiabentia pflanzii
39 CONV Ipomoea hieronymi
40 SANT Acantheosyris falcata
41 LEGP Coursetia hassleri
42 ASTE Tessaria integrifolia
43 BROM Dyckia ferox
44 CARI Jacaratia corumbensis
45 LEGM Acacia praecox
46 APOC Aspidosperma quebracho-blanco
47 LEGC Cercidium praecox
48 LEGM Acacia macracantha
49 SANT Jodina rhombifolia
50 LEGM Acacia caven
51 LEGM Acacia aroma
52 LEGM Prosopis alba
53 LEGM Acacia furcatispina
54 LEGM Prosopis chilensis
55 RHAM Condalia microphylla
56 LEGM Prosopis torquata
57 LEGC Caesalpinia gilliesii
58 ULMA Celtis tala
59 ERYT Erythroxylum microphyllum
60 LEGM Acacia bonariensis
61 CELA Maytenus vitis-idaea
62 SOLA Grabowskia duplicata
63 CAPP Capparis atamisquea
64 LEGC Senna aphylla
65 LEGM Mimozyganthus carinatus
66 ASTE Tessaria dodoneaefolia
67 ASTE Cyclolepis genistoides
68 ASTE Tessaria absinthioides
69 ANAC Schinus bumelioides
70 CACT Cereus aethiops
71 CACT Gymnocalycium delaetii
72 CACT Opuntia paediophila
73 ASTE Baccharis salicifolia
74 CACT Opuntia sulphurea
75 CACT Opuntia vulpina
76 CACT Pterocactus tuberosus
77 CHEN Allenrolfea vaginata
78 CHEN Atriplex argentina
79 CHEN Atriplex lampa
80 CHEN Heterostachys ritteriana
81 CHEN Suaeda divaricata
82 EUPH Euphorbia spp.
83 EUPH Jatropha macrocarpa
84 LEGC Senna acantheclada
85 LEGL Zuccagnia punctata
86 LEGM Mimosa farinosa
87 LEGM Prosopis sericantha
88 MALP Tricomaria usillo
89 MALV Sphaeralcea miniata
90 NYCT Boudainvillea spinosa
91 RANU Clematis hilarii
92 ZYGO Bulnesia schickendantzii
I
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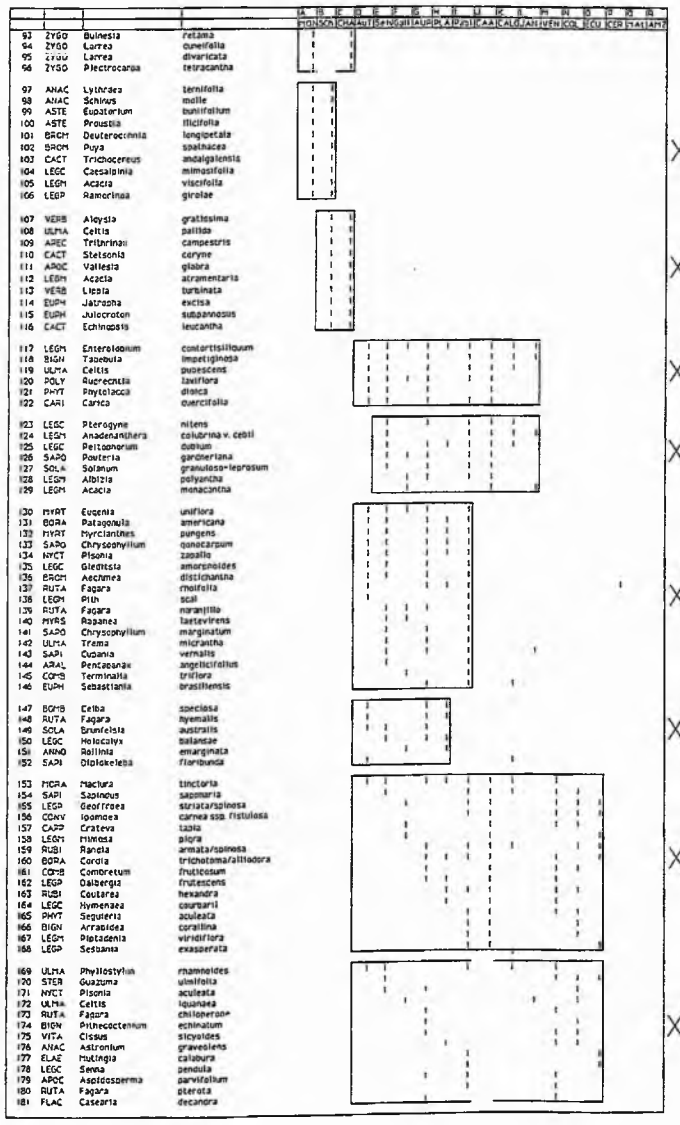
93 ZYGO Bulnesia retama
94 ZYGO Larrea cuneifolia
95 ZYGO Larrea divaricata
96 ZYGO Plectrocarpa tetracantha
97 ANAC Lythraea ternifolia
98 ANAC Schinus molle
99 ASTE Eupatorium buniifolium
100 ASTE Proustia ilicifolia
101 BROM Deuterocohnia longipetala
102 BROM Puya spathacea
103 CACT Trichocereus andalgalensis
104 LEGC Caesalpinia mimosifolia
105 LEGM Acacia viscifolia
106 LEGP Ramorinda girolae
107 VERB Aloysia gratissima
108 ULMA Celtis pallida
109 AREC Trithrinax campestris
110 CACT Stetsonia coryne
111 APOC Vallesia glabra
112 LEGM Acacia atramentaria
113 VERB Lippia turbinata
114 EUPH Jatropha excisa
115 EUPH Julocroton subpannosus
116 CACT Echinopsis leucantha
117 LEGM Enterolobium contortisiliquum
118 BIGN Tabebuia impetiginosa
119 ULMA Celtis pubescens
120 POLY Ruprechtia laxiflora
121 PHYT Phytolacca dioica
122 CARI Carica quercifolia
123 LEGC Pterogyne nitens
124 LEGM Anadenanthera colubrina v. cebil
125 LEGC Peltophorum dubium
126 SAPO Pouteria gardneriana
127 SOLA Solanum granuloso-leprosum
128 LEGM Albizia polyantha
129 LEGM Acacia monacantha
130 MYRT Eugenia uniflora
131 BORA Patagonula americana
132 MYRT Myrcianthes pungens
133 SAPO Chrysophyllum gonocarpum
134 NYCT Pisonia zapallo
135 LEGC Gleditsia amorphoides
136 BROM Aechmea distichantha
137 RUTA Fagara rhoifolia
138 LEGM Piptadenia scalt
139 RUTA Fagara naranjillo
140 MYRS Rapanea laetevirens
141 SAPO Chrysophyllum marginatum
142 ULMA Trema micrantha
143 SAPI Cupania vernalis
144 ARAL Pentapanax angelicifolius
145 COMB Terminalia triflora
146 EUPH Sebastiania brasiliensis
147 BOMB Ceiba speciosa
148 RUTA Fagara hyemalis
149 SOLA Brunfelsia australis
150 LEGC Holocalyx balansae
151 ANNO Rollinia emarginata
152 SAPI Diatenopteryx flaribunda
153 MORA Maclura tinctoria
154 SAPI Sapindus saponaria
155 LEGP Geoffroea striatarsinosa
156 CONV Ipomoea carnea ssp. fistulosa
157 CAPP Crateva tapia
158 LEGM Mimosa pigra
159 RUBI Randia armatarsonosa
160 BORA Cordia trichotomafalitadora
161 COMB Combretum fruticosum
162 LEGP Dalbergia frutescens
163 RUBI Coutarea hexandra
164 LEGC Hymenaea courbaril
165 PHYT Seguieria aculeata
166 BIGN Arrabidea corallina
167 LEGM Piptadenia viridiflora
168 LEGP Sesbania exasperata
169 ULMA Phyllostylus rhamnoides
170 STER Guazuma ulmifolia
171 NYCT Pisonia aculeata
172 ULMA Celtis iguanaea
173 RUTA Fagara chiloperone
174 BIGN Pithecoctenium echinatum
175 VITA Cissus sicyoides
176 ANAC Astronium graveolens
177 ELAE Mutingia calabura
178 LEGC Senna pendula
179 APOC Aspidosperma parvifolium
180 RUTA Fagara pterota
181 FLAC Casearia decandra
X
XI
XII
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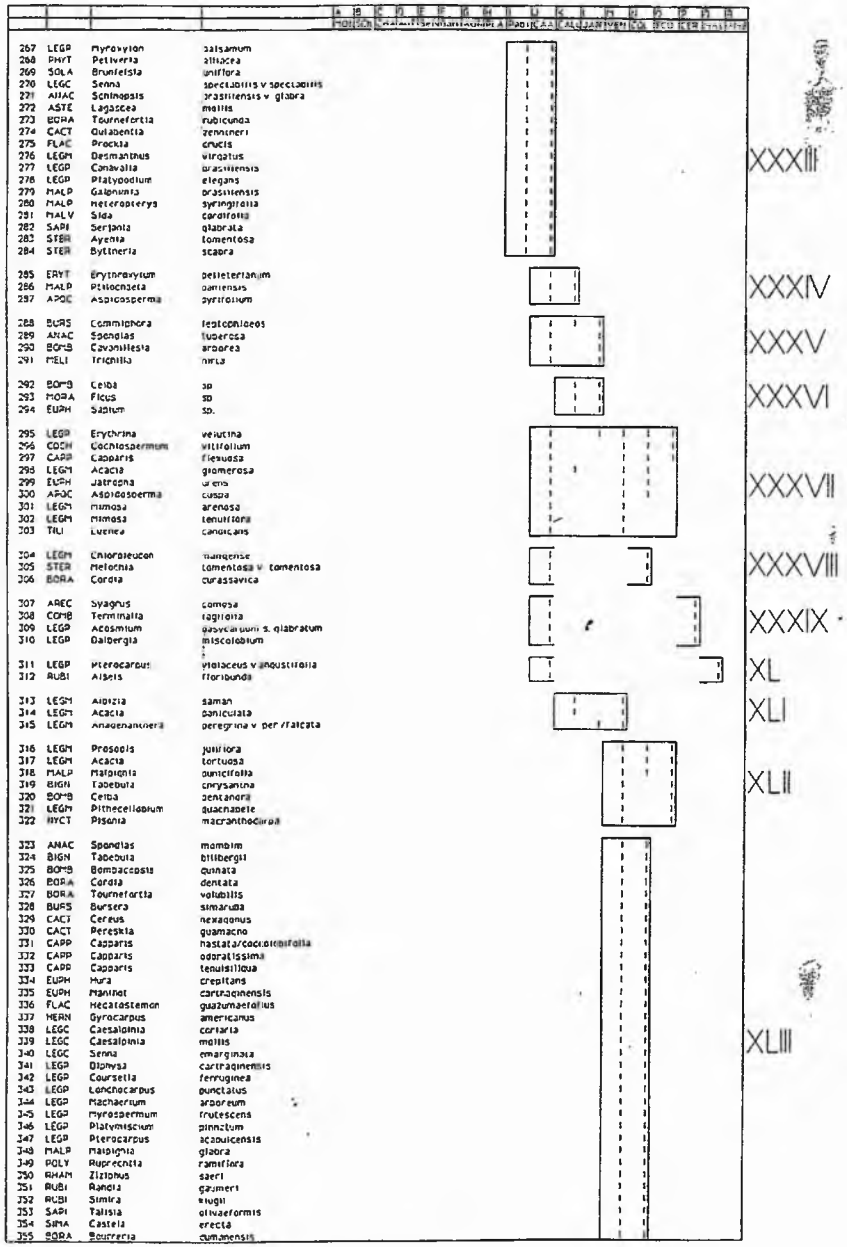
XVII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268 PHYT Petiveria alliacea
269 SOLA Brunfelsia uniflora
270 LEGC Senna spectabilis v spectabilis
271 ANAC Schinopsis brasiliensis v glabra
272 ASTE Lagascea mollis
273 BORA Tournefortia rubicunda
274 CACT Quiabentia zehntneri
275 FLAC Prockia crucis
276 LEGM Desmanthus virgatus
277 LEGP Canavalia brasiliensis
278 LEGP Platypodium elegans
279 MALP Galphimia brasiliensis
280 MALP Heteropterys syringifolia
281 MALV Sida cordifolia
282 SAPI Serjania glabrata
283 STER Ayenia tomentosa
284 STER Byttneria scabra
285 ERYT Erythroxylum pelleterianum
286 MALP Ptilochaeta bahiensis
287 APOC Aspidosperma pyrifolium
288 BURS Commiphora leptophloeos
289 ANAC Spondias tuberosa
290 BOMB Cavanillesia arborea
291 MELI Trichilia hirta
292 BOMB Ceiba sp
293 MORA Ficus sp
294 EUPH Sabium sp.
295 LEGP Erythrina velutina
296 COCH Cochlospermum vitifolium
297 CAPP Capparis flexuosa
298 LEGM Acacia glomerosa
299 EUPH Jatropha urens
300 APOC Aspidosperma cuspa
301 LEGM Mimosa arenosa
302 LEGM Mimosa tenuiflora
303 TILI Luehea candicans
304 LEGM Chloroleucon mangense
305 STER Melochia tomentosa v tomentosa
306 BORA Cordia curassavica
307 AREC Syagrus comosa
308 COMB Terminalia fagifolia
309 LEGP Acosmium dasycarpum s. glabratum
310 LEGP Dalbergia miscolobium
311 LEGP Pterocarpus violaceus v violaceus
312 RUBI Alibertia floribunda
313 LEGM Alizzia saman
314 LEGM Acacia paniculata
315 LEGM Anadenanthera peregrina v peregrina
316 LEGM Prosopis juliflora
317 LEGM Acacia tortuosa
318 MALP Mascagnia cuneifolia
319 BIGN Tabebuia chrysantha
320 BOMB Ceiba pentandra
321 LEGM Pithecellobium dulce
322 MYCT Piptadenia macrocarpa
323 ANAC Spondias mombin
324 BIGN Tabebuia billbergii
325 BOMB Bombacopsis quinata
326 BORA Cordia dentata
327 BORA Tournefortia volubilis
328 BURS Bursera simaruba
329 CACT Cereus hexagonus
330 CACT Pereskia guamacho
331 CAPP Capparis hastata/cocciloniifolia
332 CAPP Capparis odoratissima
333 CAPP Capparis tenuisiliqua
334 EUPH Hura crepitans
335 EUPH Manihot carthaginensis
336 FLAC Hecatostemon guazumaefolius
337 MORA Dyrocarpus americanus
338 LEGC Caesalpinia cortaria
339 LEGC Caesalpinia mollis
340 LEGC Senna emarginata
341 LEGP Diphysa carthaginensis
342 LEGP Coursetia ferruginea
343 LEGP Lonchocarpus punctatus
344 LEGP Machaerium arboreum
345 LEGP Myrospermum frutescens
346 LEGP Platymiscium pinnatum
347 LEGP Pterocarpus acapulcensis
348 MALP Mascagnia glabra
349 POLY Ruprechtia ramiflora
350 RHAM Ziziphus saeri
351 RUBI Randia gaumeri
352 RUBI Simira klugii
353 SAPI Talisia olivaeformis
354 SIMA Castela erecta
355 BORA Bourreria cumanensis
XXXIII
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XXXVIII
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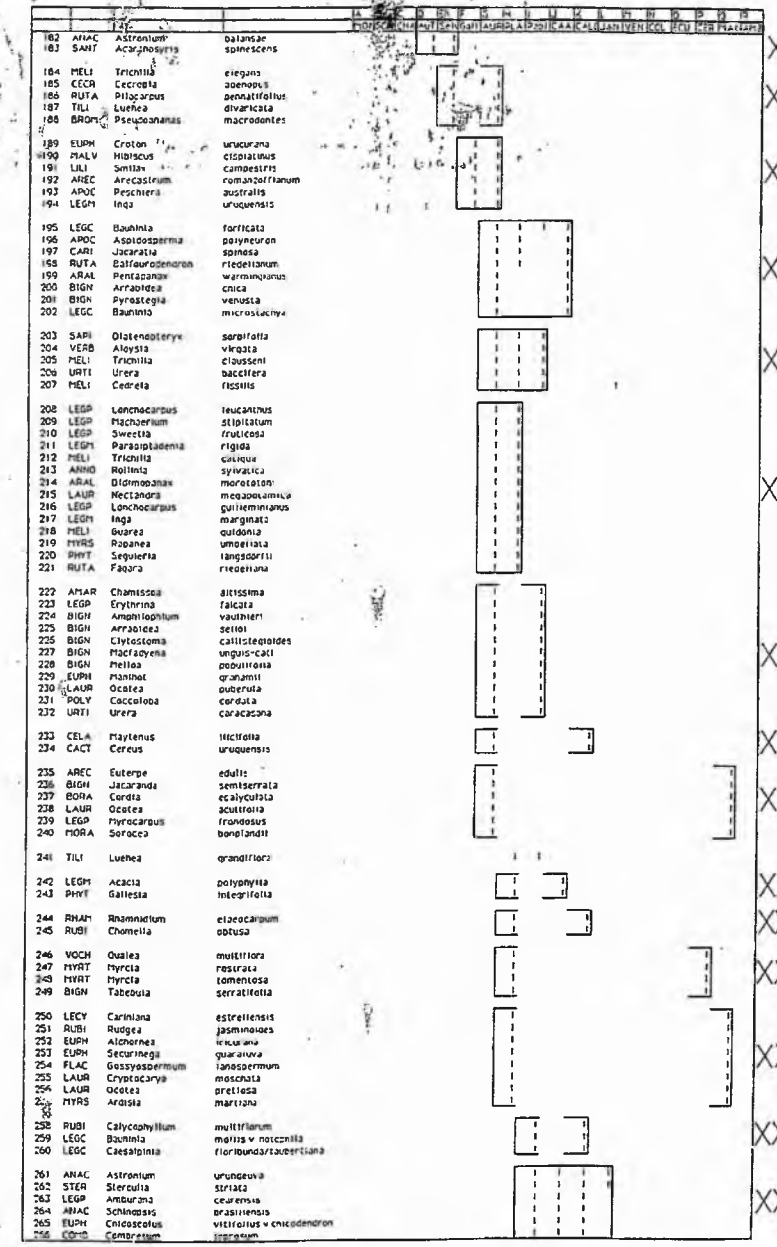

182 ANAC Astronium balansae
183 SANT Acanthosyris spinescens
184 MELI Trichilia elegans
185 CECR Cecropia adenopus
186 RUTA Pilocarpus pennatifolius
187 TILI Luehea divaricata
188 BROM Pseudoananas macrodontes
189 EUPH Croton urucurana
190 MALV Hibiscus cisplatinus
191 LILI Smilax campestris
192 AREC Arecastrum romanzoffianum
193 APOC Peschiera australis
194 LEGM Inga uruguensis
195 LEGC Bauhinia forficata
196 APOC Aspidosperma polyneuron
197 CARI Jacaratia spinosa
198 RUTA Balfourodendron riedelianum
199 ARAL Pentapanax warmingianus
200 BIGN Arrabidaea cinica
201 BIGN Pyrostegia venusta
202 LEGC Bauhinia microstachya
203 SAPI Dilodendron bipinnatum
204 VERB Aloysia virgata
205 MELI Trichilia claussenii
206 URTI Urera baccifera
207 MELI Cedrela fissilis
208 LEGP Lonchocarpus leucanthus
209 LEGP Machaerium stipitatum
210 LEGP Sweetia fruticosa
211 LEGM Parapiptadenia rigida
212 MELI Trichilia catigua
213 ANNO Rollinia sylvatica
214 ARAL Didymopanax morototoni
215 LAUR Nectandra megapotamica
216 LEGP Lonchocarpus guilleminianus
217 LEGM Inga marginata
218 MELI Guarea guidonia
219 MYRS Rapanea umbellata
220 PHYT Seguieria langsdorffii
221 RUTA Fagara riedeliana
222 MALV Chamissoa altissima
223 LEGP Erythrina falcata
224 BIGN Amphilophium vauthieri
225 BIGN Arrabidaea selloi
226 BIGN Clytostoma callistegioides
227 BIGN Macfadyena unguis-cati
228 BIGN Mansoa pubiflora
229 EUPH Manihot granamii
230 LAUR Ocotea puberula
231 POLY Coccoloba cordata
232 URTI Urera caracasana
233 CELA Maytenus ilicifolia
234 CACT Cereus uruguensis
235 AREC Euterpe edulis
236 BIGN Jacaranda semiserrata
237 BORA Cordia ecalyculata
238 LAUR Ocotea acutifolia
239 LEGP Pterocarpus frondosus
240 MORA Sorocea bonplandii
241 TILI Luehea grandiflora
242 LEGM Acacia polyphylla
243 PHYT Gallesia integrifolia
244 RHAM Rhamnidium elaeocarpum
245 RUBI Chomelia obtusa
246 VOCH Qualea multiflora
247 MYRT Myrcia rostrata
248 MYRT Myrcia tomentosa
249 BIGN Tabebuia serratifolia
250 LECY Cariniana estrellensis
251 RUBI Rudgea jasminoides
252 EUPH Alchornea iricurana
253 EUPH Securinega guaraiuva
254 FLAC Gossypospermum lanosperma
255 LAUR Cryptocarya moschata
256 LAUR Ocotea pretiosa
257 MYRS Ardisia martiana
258 RUBI Calycophyllum multiflorum
259 LEGC Bauhinia mollis v notocalla
260 LEGC Caesalpinia floribunda/taubertiana
261 ANAC Astronium urundeuva
262 STER Sterculia striata
263 LEGP Amburana cearensis
264 ANAC Schinopsis brasiliensis
265 EUPH Cnidoscolus vitifolius v vitifolius
266 COMB Combretum leprosum
XVIII
XIX
XX
XXI
XXII
XXIII
XXIV
XXV
XXVI
XXVII
XXVIII
XXIX
XXX
XXXI
XXXII

356	BORA	Pseudonomba	septentrium	
357	CAPP	Belencita	nemorosa	
358	CAPP	Morisonia	americana	
359	CAPP	Capparis	pachaca	
360	CAPP	Capparis	indica	
361	CAPP	Capparis	linearis	
362	THEO	Jacquinia	revoluta	
363	LEGC	Haematoxylon	brasiletto	
364	BURS	Bursera	tomentosa	
365	FLAC	Casearia	tremula	
366	LEGM	Pithecellobium	dulce	
367	LEGM	Acacia	rievinsa	
368	BURS	Bursera	graveolens	
369	FLAC	Casearia	silvestris	
370	LEGC	Copaifera	langsdorffii	
371	BIGN	Cydistax	antisyphylitica	
372	ERYT	Erythroxylum	deciduum	
373	BIGN	Tabebuia	caraiba	
374	BIGN	Tabebuia	aenaceа	
375	LEGP	Machaerium	acutifolium	
376	APOC	Aspidosperma	tomentosum	
377	ANAC	Astronium	fraxinifolium	
378	OPIL	Agonandra	brasiliensis	
379	BIGN	Tabura	amazonica	
380	EUPH	Pera	glabrata	
381	ELAE	Sloanea	guianensis	
382	MELI	Cabralea	canjerana	
383	BORA	Cordia	glabrata	
384	MELI	Trichilia	weddellii	
385	ACAN	Diclipiera	acutellata	I
386	ACAN	Justicia	platicarpa	I
387	ANAC	Schinus	jonnstonii	I
388	ASTE	Baccharis	angulata	I
389	ASTE	Chuquiraga	calchaquina	I
390	ASTE	Chuquiraga	erinacea	I
391	ASTE	Chuquiraga	hystrix	I
392	ASTE	Chuquiraga	straminea	I
393	ASTE	Eupatorium	patens	I
394	ASTE	Flourensia	polyciada	I
395	ASTE	Flourensia	tortuosa	I
396	ASTE	Gochnatia	glutinosa	I
397	ASTE	Heterothalamus	spartioides	I
398	ASTE	Hyaloseris	rubicunda	I
399	ASTE	Pseudobaccharis	spartioides	I
400	BROM	Abromeitiella	brevifolia	I
401	BROM	Abromeitiella	lorentziana	I
402	BROM	Deuterocohnia	schreiteri	I
403	BUDD	Buddleja	tucumanensis	I
404	CACT	Opuntia	bruchii	I
405	CACT	Opuntia	geomerica	I
406	CACT	Opuntia	glomerata	I
407	CACT	Opuntia	microdasys	I
408	CACT	Opuntia	stroblformis	I
409	CACT	Opuntia	weberi v. dispar	I
410	CACT	Trichocereus	huasche	I
411	CACT	Trichocereus	pasacana	I
412	CACT	Trichocereus	schickendantzii	I
413	CACT	Trichocereus	strigosus	I
414	CELA	Maytenus	boaria	I
415	CONV	Ipomoea	calchaquina	I
416	CONV	Ipomoea	minuta	I
417	EPHE	Ephedra	breana	I
418	EUPH	Colliguaya	integerrima	I
419	EUPH	Jatropha	gelranol	I
420	LEGC	Caesalpinia	esilifolia	I
421	LEGC	Caesalpinia	pumilla	I
422	LEGC	Hoffmannseggia	falcaria	I
423	LEGC	Senna	crassiramea	I
424	LEGC	Senna	rigida	I
425	LEGM	Mimosa	epicaroides	I
426	LEGM	Prosopis	alpataco	I
427	LEGM	Prosopis	flexuosa	I
428	LEGM	Prosopis	strombulifera	I
429	LEGM	Prosopistrum	glandosum	I
430	LEGP	Adesmia	horrida	I
431	LEGP	Adesmia	inflexa	I
432	POLG	Bredemeyera	colletioides	I
433	POLG	Bredemeyera	microphylla	I
434	RHAM	Discaria	serratifolia	I
435	RHAM	Discaria	trinervis	I
436	SCRO	Monttea	aphylla	I
437	SOLA	Fabiana	denta	I
438	SOLA	Lycium	ciliatum	I
439	SOLA	Lycium	chilense	I
440	SOLA	Lycium	decipiens	I
441	SOLA	Nicotiana	glauca	I
442	VERB	Acantholippia	deserticola	I
443	VERB	Aloysia	castellanosii	I
444	VERB	Neosparton	ephedroides	I
445	VERB	Verbena	aristocarpa	I
446	VERB	Verbena	aspera	I
447	VERB	Verbena	connatibracteata	I
448	VERB	Verbena	juniperina	I
449	VERB	Verbena	serrtifolioides	I
450	ZYGO	Larrea	americanoi	I

XLIV

XLV

XLVI

XLVII

451	ZYGO	Larrea	nitida	I
452	ZYGO	Plectrocarpa	rougesii	I
453	ANAC	Schinus	praecox	I
454	ASTE	Baccharis	articulata	I
455	ASTE	Baccharis	flabellata	I
456	ASTE	Baccharis	myrtilloides	I
457	ASTE	Eupatorium	argentinum	I
458	ASTE	Eupatorium	viscidum	I
459	ASTE	Flourensia	oolepis	I
460	ASTE	Flourensia	campestris	I
461	ASTE	Heterothalamus	alienus	I
462	ASTE	Ophryosporus	axilliflorus	I
463	BERB	Berberis	hieronymi	I
464	BUDD	Buddleja	cordobensis	I
465	BUDD	Buddleja	mendozensis	I
466	CACT	Acanthocalycium	violaceum	I
467	CACT	Gymnocalycium	capillense	I
468	CACT	Gymnocalycium	multiflorum	I
469	CACT	Trichocereus	candicans	I
470	EUPH	Acalypha	poiretii	I
471	EUPH	Stillingia	bodenbenderi	I
472	FLAC	Banara	umbraticola	I
473	LABI	Hinthostachys	mollis	I
474	LEGM	Prosopis	campestris	I
475	LEGM	Prosopis	humilis	I
476	LEGP	Aparimazia	dolichocarpa	I
477	LEGP	Calliaea	argentina	I
478	LEGP	Psoralea	higueritia	I
479	LEGP	Sophora	linearifolia	I
480	LOBE	Siphocampylus	folliosus	I
481	MALP	Cordobia	argentea	I
482	MALP	Mionandra	camareoides	I
483	POLG	Monnina	dictyocarpa	I
484	RHAM	Colletia	spinosissima	I
485	RHAM	Condalia	buxifolia	I
486	RHAM	Condalia	montana	I
487	ROSA	Kageneckia	lanceolata	I
488	SCRO	Monttea	schickendantzii	I
489	STER	Ayenia	cordobensis	I
490	VERB	Aloysia	catamarcensis	I
491	VERB	Aloysia	scordodonioides v scaroa	I
492	SIMA	Castela	coccinea	I
493	ANAC	Schinopsis	balansae	I
494	BIGN	Tabebuia	nodosa	I
495	LEGM	Prosopis	affinis	I
496	ANAC	Schinopsis	quebracho-colorada	I
497	LEGM	Prosopis	kuntzei	I
498	CELA	Maytenus	spinosa	I
499	ANAC	Schinopsis	heterophylla	I
500	SOLA	Cestrum	parqui	I
501	CHEN	Holmbergia	tweediei	I
502	CACT	Opuntia	chakensis	I
503	CACT	Monvillea	cavendishii	I
504	CACT	Eriocereus	tortuosus	I
505	CACT	Echinopsis	minuana	I
506	POLY	Fuoreretia	triflora	I
507	CAPP	Capparis	salicifolia	I
508	CAPP	Capparis	speciosa	I
509	CACT	Opuntia	colubrina	I
510	CACT	Eriocereus	pomanensis	I
511	ZYGO	Bulnesia	foliosa	I
512	LEGM	Mimosa	detinens	I
513	NYCT	Bougainvillea	campanulata	I
514	BROM	Bromelia	hieronymi	I
515	LEGM	Prosopis	vinalillo	I
516	LEGM	Prosopis	ruscifolia	I
517	SOLA	Lycium	sp.	I
518	AREC	Trithrinax	biflabellata	I
519	ASTE	Hyalis	lanciifolia	I
520	ANAC	Schinopsis	cermuta	I
521	APOC	Aspidosperma	triternatum	I
522	ASCL	Marsdenia	castillonii	I
523	ASTE	Baccharis	notosergila	I
524	BERB	Berberis	ruscifolia	I
525	BIGN	Dolichandra	cynanchoides	I
526	BIGN	Mansoa	truncata	I
527	BIGN	Pithecoctenium	cynanchoides	I
528	BORA	Cortesia	cuneifolia	I
529	BROM	Bromelia	urbaniana	I
530	BROM	Dyckia	tweedieі	I
531	BROM	Dyckia	ragonesei	I
532	BUDD	Buddleja	brasiliensis	I
533	BUDD	Buddleja	stachyoides	I
534	CACT	Castellanosia	caineana	I
535	CACT	Cereus	comarapaanus	I
536	CACT	Cereus	forbesii	I
537	CACT	Cleistocactus	baumannii	I
538	CACT	Cleistocactus	brunispinus	I
539	CACT	Cleistocactus	flavispinus	I
540	CACT	Echinopsis	chacoana	I
541	CACT	Echinopsis	shaferi	I
542	CACT	Eriocereus	bonplandii	I
543	CACT	Eriocereus	guelichii	I
544	CACT	Eriocereus	martinii	I
545	CACT	Gymnocalycium	ragonesei	I
546	CACT	Gymnocalycium	friedrichii	I
547	CACT	Gymnocalycium	mihanovichii	I
548	CACT	Gymnocalycium	pflanzii	I
549	CACT	Gymnocalycium	megatae	I
550	CACT	Monvillea	pajanziana	I

				A MON	B Sch	C CHA	D Aut	E Se	F Gall	G AUR	H PLA	I Pab	J CAA	K CAL	L JUA	M VEN	N COL	O ECU	P CER	Q MAI	R AM2
551	CACT	Monvillea	spegazzinii																		
552	CACT	Opuntia	aurantiaca																		
553	CACT	Opuntia	discolor																		
554	CACT	Opuntia	brunnescens																		
555	CACT	Opuntia	kiskalora																		
556	CACT	Opuntia	pampeana																		
557	CACT	Opuntia	quimilo																		
558	CACT	Opuntia	retrorsa																		
559	CACT	Opuntia	salagria																		
560	CACT	Opuntia	salmiana																		
561	CACT	Setiechinopsis	mirabilis																		
562	CACT	Trichocereus	lamprochlorus																		
563	CACT	Trichocereus	spachianus																		
564	CHEN	Allenrolfea	patagonica																		
565	CHEN	Atriplex	cordobensis																		
566	CHEN	Atriplex	eximia																		
567	CHEN	Atriplex	spegazzinii																		
568	CHEN	Heterostachys	olivaceus																		
569	CHEN	Salicornia	ambigua																		
570	CONV	Ipomoea	stuckertii																		
571	EUPH	Acalypha	communis																		
572	EUPH	Croton	bonplandianum																		
573	EUPH	Croton	parvifolius																		
574	EUPH	Jatropha	chacoana																		
575	EUPH	Jatropha	flavovirens																		
576	EUPH	Jatropha	grossidentata																		
577	EUPH	Jatropha	hieronymi																		
578	EUPH	Jatropha	matacensis																		
579	LEGC	Bauhinia	argentinensis v.argentin.																		
580	LEGC	Caesalpinia	stuckertii																		
581	LEGC	Lophocarpinia	aculeatifolia																		
582	LEGC	Senna	chacoensis																		
583	LEGC	Senna	chloroclada																		
584	LEGC	Senna	morongii																		
585	LEGC	Senna	occidentalis																		
586	LEGC	Senna	spinifiora																		
587	LEGC	Stenodrepanum	bergii																		
588	LEGM	Acacia	curvifructa																		
589	LEGM	Desmanthus	brevipes																		
590	LEGM	Prosopis	abbreviata																		
591	LEGM	Prosopis	elata																		
592	LEGM	Prosopis	flebrigii																		
593	LEGM	Prosopis	hassleri																		
594	LEGM	Prosopis	pugionata																		
595	LEGM	Prosopis	reptans																		
596	LEGM	Prosopis	rojasiana																		
597	LYTH	Heimia	salicifolia																		
598	MALP	Janusia	guaranitica																		
599	MALV	Abutilon	virgatum																		
600	MALV	Pavonia	argentina																		
601	MALV	Sida	argentina																		
602	MALV	Sida	dictyocarpa																		
603	MALV	Sida	spinosa																		
604	MALV	Sphaeralcea	bonariensis																		
605	MALV	Wissadula	densiflora																		
606	MENI	Cissampelos	pareira v. gardneri																		
607	MENI	Odontocarya	asarifolia																		
608	MENI	Odontocarya	thamnoides																		
609	NYCT	Bougainvillea	infesta																		
610	NYCT	Bougainvillea	praecox																		
611	OLEA	Menodora	integrifolia																		
612	PORT	Amphipetalum	paraguayense																		
613	PORT	Grahamia	bracteata																		
614	RANU	Clematis	montevidensis																		
615	SAPI	Urvillea	uniloba																		
616	SOLA	Capsicum	chacoense																		
617	SOLA	Grabowskia	obtusa																		
618	SOLA	Lycium	americanum																		
619	SOLA	Solanum	argentinum																		
620	SOLA	Solanum	chrysotrichum																		
621	SOLA	Solanum	diflorum																		
622	SOLA	Solanum	glaucophyllum																		
623	STER	Ayenia	acalyphifolia																		
624	STER	Ayenia	ellae																		
625	STER	Ayenia	lingulata																		
626	STER	Ayenia	o'donellii																		
627	VERB	Aloysia	polystachia																		
628	VERB	Lippia	integrifolia																		
629	VERB	Lippia	salsa																		
630	VERB	Xeroaloysia	ovatifolia																		
631	ZYGO	Bulnesia	bonariensis																		
632	ZYGO	Bulnesia	sarmientoi																		
633	MORA	Ficus	luschnathiana																		
634	CELA	Schaefferia	argentinensis																		
635	CAPP	Capparis	aff. retusa?																		
636	MORA	Sorocea	sprucei																		
637	PTER	Acrostichum	aureum																		
638	LAUR	Nectandra	falcifolia																		
639	LEGP	Erythrina	crista-galli																		
640	MYRT	Hexachlamis	edulis																		
641	FLAC	Banara	arguta																		
642	AMAR	Chamissoa	macrocarpa																		
643	ANNO	Rollinia	exalbida																		
644	ANNO	Rollinia	rugulosa																		
645	ANNO	Rollinia	salicifolia																		
646	APOC	Rauvolfia	sellowii																		
647	AQUI	Ilex	paraguariensis																		
648	BIGN	Adenocalymma	marginatum																		
649	BIGN	Arrabidea	mutabilis																		
650	BIGN	Clytostoma	binatum																		

				A MON	B Sch	C CHA	D Aut	E Se	F Gall	G AUR	H PLA	I Pab	J CAA	K CAL	L JUA	M VEN	N COL	O ECU	P CER	Q MAI	R AM2
651	BIGN	Clytostoma	uniflorum																		
652	BIGN	Cuspidaria	pterocarpa																		
653	BIGN	Jacaranda	micrantha																		
654	BIGN	Jacaranda	puberula																		
655	BIGN	Macfadyena	dentata																		
656	BIGN	Tabebuia	alba																		
657	BIGN	Tabebuia	pulcherrima																		
658	BORA	Cordia	discolor																		
659	BORA	Tournefortia	breviflora																		
660	BORA	Tournefortia	paniculata																		
661	BROM	Bilbergia	nutans																		
662	BROM	Bromelia	balansae																		
663	CACT	Pereskia	aculeata																		
664	CAPR	Sambucus	australis																		
665	CELA	Maytenus	aquifolium																		
666	CELA	Maytenus	dasyclados																		
667	COMB	Terminalia	australis																		
668	ERYT	Erythroxylum	amplifolium																		
669	ERYT	Erythroxylum	myrsinites																		
670	EUPH	Actinostemon	concolor																		
671	EUPH	Alchornea	sidifolia																		
672	EUPH	Alchornea	triplinervia																		
673	EUPH	Pachystroma	longifolium																		
674	EUPH	Phyllanthus	sellowianus																		
675	EUPH	Sapium	petiolare																		
676	EUPH	Sebastiania	schottiana																		
677	EUPH	Tetrorchidium	rubrivenium																		
678	FLAC	Banara	parviflora																		
679	FLAC	Banara	tomentosa																		
680	FLAC	Casearia	inaequilatera																		
681	FLAC	Xylosma	ciliatifolium																		
682	FLAC	Xylosma	prockia																		
683	ICAC	Citronella	cuspidata																		
684	LAUR	Nectandra	grandiflora																		
685	LAUR	Nectandra	lanceolata																		
686	LAUR	Nectandra	rigida																		
687	LAUR	Nectandra	tweedlei																		
688	LAUR	Ocotea	diospyrifolia																		
689	LEGC	Apuleia	leiocarpa																		
690	LEGP	Ateleia	glazioviana																		
691	LEGP	Dahlstedtia	pinnata																		
692	LEGP	Dioclea	megacarpa																		
693	LEGP	Lonchocarpus	muehlbergianus																		
694	LEGP	Lonchocarpus	nitidus																		
695	LEGP	Machaerium	aculeatum																		
696	LEGP	Machaerium	nyctitans																		
697	LEGP	Poecilanthe	parviflora																		
698	LEGM	Acacia	nitidifolia																		
699	LEGM	Acacia	recurva																		
700	LEGM	Acacia	velutina																		
701	LEGM	Calliandra	foliosa																		
702	LEGM	Calliandra	selloi																		
703	LEGM	Inga	affinis v.catharinensis																		
704	LEGM	Inga	sessilis																		
705	LEGM	Inga	virescens																		
706	LEGM	Pithecellobium	hassleri																		
707	LEGM	Zygia	glomerata																		
708	LILI	Cordyline	dracaenoides																		
709	LOGA	Strychnos	brasiliensis																		
710	MALV	Bastardiopsis	densiflora																		
711	MELI	Guarea	lessoniana																		
712	MONI	Hennecartia	omphalandra																		
713	MONI	Mollinedia	elegans																		
714	MORA	Ficus	diabolica																		
715	MORA	Ficus	insipida																		
716	MORA	Ficus	organensis																		
717	MYRT	Calyptranthes	concinna																		
718	MYRT	Calyptranthes	tricona																		
719	MYRT	Campomanesia	guazumaefolia																		
720	MYRT	Campomanesia	xanthocarpa																		
721	MYRT	Eugenia	involucrata																		
722	MYRT	Eugenia	moraviana																		
723	MYRT	Eugenia	pyriformis																		
724	MYRT	Eugenia	ramboi																		
725	MYRT	Eugenia	rostrifolia																		
726	MYRT	Eugenia	uruguayensis v. urug.																		
727	MYRT	Gomidesia	affinis v. catharinensis																		
728	MYRT	Myrceugenia	glaucescensv.glaucescens																		
729	MYRT	Myrcia	laruotteana v paraguayen.																		
730	MYRT	Myrciaria	tenella																		
731	PIPE	Piper	gaudichaudianum																		
732	PIPE	Piper	longipes																		
733	PIPE	Piper	parthenium																		
734	PROT	Roupala	cataractarum																		
735	PROT	Roupala	meisneri																		
736	RUBI	Faramea	porophylla																		
737	RUBI	Guettarda	uruguensis																		
738	RUTA	Esenbeckia	grandiflora																		
739	RUTA	Helietta	longifoliata																		
740	SAPI	Allophyllus	guaraniticus																		
741	SAPI	Matayba	elaeagnoides																		
742	SAPI	Paullinia	elegans																		
743	SAPI	Paullinia	trigonia																		
744	SAPO	Pouteria	salicifolia																		
745	SIMA	Castela	tweedlei																		
746	SIMA	Picramnia	parvifolia																		
747	SIMA	Picrasmia	crenata																		
748	SOLA	Cestrum	calycinum																		
749	SOLA	Cestrum	intermedium																		
750	STER	Byttneria	australis																		

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				PIGN	SCH	CHA	LAU	TSE	NGA	ITA	URI	PLA	PAB	ICA	ACA	LOJ	JAN	VEN	COL	ECU	CER	HAI	AMZ
751	STER	Byttneria	urticifolia																				
752	URTI	Boehmeria	caudata																				
753	THYM	Daphnopsis	racemosa																				
754	VERB	Aegiphila	brachiata																				
755	VERB	Aegiphila	hassleri																				
756	VERB	Vitex	megapotamica																				
757	ANNO	Annona	cacans																				
758	APOC	Peschiera	fuchsiaefolia																				
759	BURS	Protium	heptaphyllum																				
760	EUPH	Croton	floribundus																				
761	FLAC	Casearia	gossyposperma																				
762	LAUR	Endlicheria	paniculata																				
763	LAUR	Ocotea	catharinensis																				
764	LEGC	Bauhinia	fusconervis																				
765	LEGP	Centrolobium	tomentosum																				
766	LEGM	Piptadenia	gonoacantha																				
767	LEGM	Pithecellobium	edwallii																				
768	MONI	Mollinedia	widgrenii																				
769	MORA	Ficus	sp.																				
770	MYRS	Ardisia	ambigua																				
771	MYRT	Campomanesia	guavirova																				
772	MYRT	Psidium	guajava																				
773	AREC	Acrocomia	aculeata																				
774	PROT	Roupala	brasiliensis																				
775	RUTA	Metrodorea	nigra																				
776	RUTA	Fagara	pohliana																				
777	TILI	Christiana	macrmacrodon																				
778	VERB	Aegiphila	sellowiana																				
779	APOC	Aspidosperma	cyilindrocarpon																				
780	APOC	Aspidosperma	ramiflorum																				
781	ASTE	Piptocarpha	macropoda																				
782	ASTE	Vernonia	diffusa																				
783	BIGN	Tabebuia	vellosoi																				
784	BIGN	Zeyhera	tuberculosa																				
785	CLUS	Callophyllum	brasiliense																				
786	EUPH	Acalypha	villosa																				
787	EUPH	Actinostemon	estrellensis																				
788	EUPH	Actinostemon	klotzschii																				
789	EUPH	Actinostemon	sp.																				
790	EUPH	Croton	salutaris																				
791	LACI	Lacistema	floribundum																				
792	LECY	Cariniana	legalis																				
793	LEGC	Dimorphandra	exaltata																				
794	LEGP	Platycyamus	regnellii																				
795	LEGM	Inga	edulis																				
796	LEGM	Inga	striata																				
797	MELA	Miconia	sp.																				
798	MELI	Trichilia	casarettii																				
799	MELI	Trichilia	sellol																				
800	MELI	Guarea	pohlii																				
801	MONI	Mollinedia	chrysorrhachis																				
802	CECR	Cecropia	cinerea																				
803	MORA	Ficus	glabra																				
804	MYRT	Calycorectes	schottianus																				
805	MYRT	Calyptranthes	lucida v polyantha																				
806	MYRT	Eugenia	brasiliensis																				
807	MYRT	Eugenia	sp.																				
808	MYRT	Myrcia	sp.																				
809	MYRT	Siphoneugena	widgrentana																				
810	NYCT	Pisonia	olfersiana																				
811	PIPE	Piper	amalago																				
812	PIPE	Piper	arboreum																				
813	RUTA	Esenbeckia	febrifuga																				
814	SAPI	Allophyllus	sericeus																				
815	SAPI	Allophyllus	membranifolius																				
816	SIMA	Picramnia	warmingiana																				
817	SOLA	Solanum	swartzianum																				
818	STYR	Styrax	pohlii																				
819	LEGP	Tipuana	tipu																				
820	BOMB	Pseudobombax	argentinum																				
821	MELI	Cedrela	odorata																				
822	MELI	Cedrela	lilloi																				
823	LEGM	Paraplptadenia	excelsa																				
824	LEGP	Lonchocarpus	lilloi																				
825	LEGM	Acacia	albicorticata																				
826	SAPI	Athyana	weinmannifolia																				
827	AREC	Acrocomia	chonta																				
828	RUBI	Pogonopus	tubulosus																				
829	ASTE	Vernonia	fulta																				
830	ASTE	Chicothamnus	lorentzii																				
831	BUDD	Buddleja	albotomentosa																				
832	ANAC	Loxopterigium	grisebachii																				
833	BIGN	Jacaranda	mimosifolia																				
834	MYRT	Myrciantnes	mato																				
835	BIGN	Tecoma	stans																				
836	PIPE	Piper	tucumanum																				
837	TILI	Heliocarpus	popayanensis																				
838	ANAC	Schinus	gracilipes																				
839	ANAC	Schinus	venturii																				
840	ANNO	Rollinia	occidentalis																				
841	APOC	Rauvolfia	schuelli																				
842	AREC	Trithrinax	schizophylla																				
843	ASCL	Marsdenia	altissima																				
844	ASCL	Schubertia	schreiteri																				
845	BIGN	Amphilophium	sandwithii																				
846	BIGN	Jacaranda	cuspidifolia																				
847	BIGN	Paradolichandra	chodatii																				
848	BOMB	Eriotheca	roseorum																				
849	BORA	Saccellium	lanceolatum																				
850	BORA	Tournefortia	lilloi																				

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				PIGN	SCH	CHA	LAU	TSE	NGA	ITA	URI	PLA	PAB	ICA	ACA	LOJ	JAN	VEN	COL	ECU	CER	HAI	AMZ
851	CACT	Brasiliopuntia	brasiliensis																				
852	CACT	Espostoa	quentheri																				
853	CACT	Opuntia	sp.																				
854	CACT	Quiabentia	verticillata																				
855	CACT	Trichacereus	thelegonoides																				
856	CARI	Carica	glandulosa																				
857	CELA	Maytenus	cuezzoi																				
858	CELA	Plenckia	integerrima																				
859	COCH	Cochlospermum	tetraporum																				
860	COMB	Combretum	guanalense																				
861	ASTE	Barnadesia	odorata																				
862	ASTE	Chaenocephalus	heterophyllus																				
863	ASTE	Dasyphyllum	brasiliense																				
864	ASTE	Eupatorium	laslophthalmum																				
865	ASTE	Eupatorium	saltense																				
866	ASTE	Pseudogynoxys	benthamii																				
867	ASTE	Senecio	deferrens																				
868	ASTE	Senecio	peregrinus																				
869	ASTE	Vernonia	cincta																				
870	ASTE	Vernonia	squamulosa																				
871	CONV	Ipomoea	crinicalyx																				
872	ERYT	Erythroxylum	argentinum																				
873	ERYT	Erythroxylum	cuneifolium																				
874	EUPH	Croton	beetlei																				
875	EUPH	Croton	densiflorus																				
876	EUPH	Ditaxis	breviramea																				
877	EUPH	Euphorbia	oranensis																				
878	EUPH	Jatropha	hieronymi																				
879	EUPH	Manihot	anomala ssp. pavoniana																				
880	EUPH	Manihot	guaranitica s.guaranitica																				
881	EUPH	Parodiodendron	marginivillosum																				
882	EUPH	Phyllanthus	acuminatus																				
883	LAUR	Phoebe	porphyria																				
884	LEGC	Bauhinia	argentinensis v megasiph																				
885	LEGC	Chamaecrista	calycioides v calycioides																				
886	LEGC	Copaifera	paupera																				
887	LEGM	Acacia	etilis																				
888	LEGM	Acacia	parviceps																				
889	LEGM	Calliandra	formosa																				
890	LEGM	Inga	saltensis																				
891	LEGM	Mimosa	polycarpa																				
892	LEGM	Mimosa	sensibilis																				
893	LEGM	Mimosa	stenoptera																				
894	LEGM	Mimosa	velloziana																				
895	LEGM	Pithecellobium	chacoense																				
896	LEGM	Pithecellobium	grisebachianum																				
897	LEGP	Aeschynomene	rudis																				
898	LEGP	Cascaronia	astragalina																				
899	LEGP	Coursetia	brachyrhachis																				
900	LEGP	Coursetia	hypoleuca																				
901	LEGP	Erythrina	dominguezii																				
902	LEGP	Swartzia	jorori																				
903	MALP	Heteropterys	sylvatica																				
904	MALP	Heteropterys	umbellata																				
905	MALP	Ptilochaeta	nudipes																				
906	MALP	Stigmatophyllon	coloratum																				
907	MALV	Abutilon	molle																				
908	MALV	Pavonia	eurychlamys																				
909	MALV	Pavonia	hirta																				
910	MALV	Pavonia	malvacea																				
911	MORA	Ficus	maroma																				
912	MYRT	Siphoneugena	occidentalis																				
913	NYCT	Pisoniella	arborescens v glabrata																				
914	OLAC	Schoepfia	tetramera																				
915	OPIL	Agonandra	excelsa																				
916	PHYT	Hillería	latifolia																				
917	PHYT	Phytolacca	bogotensis																				
918	PHYT	Seguieria	paraguayensis																				
919	PIPE	Piper	aduncum v.corodulatum																				
920	PIPE	Piper	medium																				
921	POLY	Coccoloba	tiliacea																				
922	RHAM	Ziziphus	oblongifolius																				
923	RHAM	Ziziphus	plurensis																				
924	RUBI	Hoffmannia	australis																				
925	RUBI	Manettia	cordifolia																				
926	RUTA	Fagara	nigrescens																				
927	SAPI	Diplokeleba	herzogi																				
928	SCRO	Basistemon	silvaticus																				
929	SCRO	Basistemon	spinosus																				
930	SIMA	Alvaradoa	puberulenta																				
931	SOLA	Cestrum	lorentzianum																				
932	SOLA	Lycium	cestroides																				
933	STER	Ayenia	subtilis																				
934	STER	Byttneria	oranensis																				
935	STER	Byttneria	tucumanensis																				
936	STER	Melochia	argentina																				
937	ULMA	Celtis	chichape																				
938	VERB	Aloysia	triphylla																				
939	VERB	Lantana	fiebrigii																				
940	VERB	Lantana	trifolia																				
941	VERB	Lippia	grisebachiana																				
942	VERB	Lippia	suffruticosa																				
943	ANAC	Astronium	concinnum																				
944	ANAC	Loxopterigium	gardneri																				
945	ANNO	Annona	spinescens																				
946	ANNO	Annona	vepertorum																				
947	ANNO	Rollinlopsis	leptopetala																				
948	APOC	Allamanda	blanchetii																				
949	APOC	Allamanda	martii																				
950	APOC	Allamanda	puberula																				

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				MONSCh	CHAJAUTI	SeNGalli	AURPLA	PasIC	AACALQUA	JANIVENICOL	ECU	CER	MATIAM2								
951	APOC	Allamanda	oenotherifolia																		
952	APOC	Aspidosperma	discolor																		
953	APOC	Aspidosperma	riedelii subsp.longanthum																		
954	APOC	Rauvolfia	paucifiora																		
955	APOC	Skytanthus	hancorniaefolius																		
956	AREC	Copernicia	cerifera																		
957	AREC	Syagrus	coronata																		
958	AREC	Syagrus	microphylla																		
959	AREC	Syagrus	oleracea																		
960	AREC	Syagrus	vagans																		
961	AREC	Syagrus	wedermannii																		
962	AREC	Syagrus	X matafome																		
963	ASTE	Blanchetia	heterotricha																		
964	ASTE	Dasyphyllum	candolleanum																		
965	ASTE	Eremanthus	marcii																		
966	ASTE	Pectis	decumbens																		
967	ASTE	Pectis	elongata																		
968	ASTE	Pectis	linifolia v.linifolia																		
969	ASTE	Telmatophila	scolymastrum																		
970	ASTE	Wunderlichia	cruisiana																		
971	BIGN	Anemopaegna	velutinum																		
972	BIGN	Cuspidaria	argentea																		
973	BIGN	Godmania	dardanoi																		
974	BIGN	Jacaranda	irwinii																		
975	BIGN	Jacaranda	jasminoides																		
976	BIGN	Tabebuia	roseo-alba																		
977	BIGN	Tabebuia	spongiosa																		
978	BOMB	Ceiba	glaziovii																		
979	BOMB	Eriotheca	parvifolia																		
980	BOMB	Pseudobombax	simplicifolium																		
981	BORA	Auxemma	glazioviana																		
982	BORA	Auxemma	oncocalyx																		
983	BORA	Cordia	dardani																		
984	BORA	Cordia	glabosa																		
985	BORA	Cordia	insignis																		
986	BORA	Cordia	leucocephala																		
987	BORA	Patagonula	bahiensis																		
988	BROM	Aechmea	eurycorymbus																		
989	BROM	Aechmea	aquilega v chrysocoma																		
990	BROM	Aechmea	lingulata																		
991	BROM	Billbergia	porteana																		
992	BROM	Bromelia	laciniosa																		
993	BROM	Cottendorfia	florida																		
994	BROM	Dyckia	dissitiflora																		
995	BROM	Dyckia	limae																		
996	BROM	Dyckia	pernambucana																		
997	BROM	Encholirium	spectabile																		
998	BROM	Hohenbergia	caatingae																		
999	BROM	Neoglaziovia	variegata																		
1000	BROM	Pitcairnia	flammea																		
1001	CACT	Acanthocereus	?albicaulis																		
1002	CACT	Acanthocereus	brasiliensis																		
1003	CACT	Arrojadoa	penicillata																		
1004	CACT	Arrojadoa	rhodantha																		
1005	CACT	Austrocephalocereus	dybowskii																		
1006	CACT	Austrocephalocereus	purpureus																		
1007	CACT	Brasilopuntia	bahiensis																		
1008	CACT	Cereus	jamacaru																		
1009	CACT	Discocactus	bahiensis																		
1010	CACT	Discocactus	placentiformis																		
1011	CACT	Discocactus	zehntneri																		
1012	CACT	Eriocereus	adscendens																		
1013	CACT	Espostoa	ulei																		
1014	CACT	Leocereus	bahiensis																		
1015	CACT	Melocactus	bahiensis																		
1016	CACT	Melocactus	horridus																		
1017	CACT	Melocactus	oreas																		
1018	CACT	Melocactus	zehntneri																		
1019	CACT	Micranthocereus	polyanthus																		
1020	CACT	Pereskia	aureiflora																		
1021	CACT	Pereskia	bahiensis																		
1022	CACT	Pereskia	stenantha																		
1023	CACT	Opuntia	inamoena																		
1024	CACT	Opuntia	palmadora																		
1025	CACT	Pilosocereus	catingicola																		
1026	CACT	Pilosocereus	chrysostele																		
1027	CACT	Pilosocereus	glaucescens																		
1028	CACT	Pilosocereus	gounellei																		
1029	CACT	Pilosocereus	piauhiensis																		
1030	CACT	Pilosocereus	tuberculatus																		
1031	CACT	Pilosocereus	zehntneri																		
1032	CACT	Stephanocereus	leucostele																		
1033	CACT	Tacinga	funalis																		
1034	CACT	Zehntnerella	squamulosa																		
1035	CAPP	Capparis	jacobinae																		
1036	CAPP	Capparis	yco																		
1037	CAPP	Haptocarpum	bahiense																		
1038	CARI	Jacaratia	sp																		
1039	CELA	Fraunhoffera	multiflora																		
1040	CELA	Maytenus	rigida																		
1041	CHRY	Couepia	ulei																		
1042	CHRY	Licania	rigida																		
1043	COMB	Combretum	lanceolatum																		
1044	COMB	Combretum	laxum																		
1045	COMB	Combretum	mellifluum																		
1046	COMB	Combretum	monetaria																		
1047	COMB	Combretum	pisonioides																		
1048	COMB	Combretum	rupicola																		
1049	COMB	Thilloa	glaucocarpa																		
1050	CONV	Ipomoea	agaricifolia																		

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				MONSCh	CHAJAUTI	SeNGalli	AURPLA	PasIC	AACALQUA	JANIVENICOL	ECU	CER	MATIAM2								
1051	ERYT	Erythroxylum	betulaceum																		
1052	ERYT	Erythroxylum	bezerrae																		
1053	ERYT	Erythroxylum	caatingae																		
1054	ERYT	Erythroxylum	campestre																		
1055	ERYT	Erythroxylum	flaccidum																		
1056	ERYT	Erythroxylum	maracasense																		
1057	ERYT	Erythroxylum	nummularia																		
1058	ERYT	Erythroxylum	macrochaetum																		
1059	ERYT	Erythroxylum	oxypetalum																		
1060	ERYT	Erythroxylum	petrae-caballi																		
1061	ERYT	Erythroxylum	polygonoides																		
1062	ERYT	Erythroxylum	pungens																		
1063	ERYT	Erythroxylum	revolutum																		
1064	ERYT	Erythroxylum	subrotundum																		
1065	EUPH	Alchornea	castaneaefolia																		
1066	EUPH	Cnidoscolus	bahiensis																		
1067	EUPH	Cnidoscolus	phyllacanthus																		
1068	EUPH	Croton	argyrophylloides																		
1069	EUPH	Croton	campestris																		
1070	EUPH	Croton	hemiargyreus																		
1071	EUPH	Croton	jacobinensis																		
1072	EUPH	Croton	micans																		
1073	EUPH	Croton	sincorensis																		
1074	EUPH	Croton	sonderianus																		
1075	EUPH	Croton	tricolor																		
1076	EUPH	Croton	zehntneri																		
1077	EUPH	Ditaxis	desertorum																		
1078	EUPH	Ditaxis	malpighiacea																		
1079	EUPH	Euphorbia	phosphorea																		
1080	EUPH	Jatropha	mutabilis																		
1081	EUPH	Jatropha	pohliana																		
1082	EUPH	Jatropha	ribifolia																		
1083	EUPH	Manihot	brachyandra																		
1084	EUPH	Manihot	caerulescens s. caerul.																		
1085	EUPH	Manihot	catingae																		
1086	EUPH	Manihot	dichotoma																		
1087	EUPH	Manihot	epruinosa																		
1088	EUPH	Manihot	glaziovii																		
1089	EUPH	Manihot	heptaphylla																		
1090	EUPH	Manihot	maracasensis																		
1091	EUPH	Manihot	pseudoglaziovii																		
1092	EUPH	Maprounea	brasiliensis																		
1093	EUPH	Maprounea	guyanensis																		
1094	EUPH	Sapium	montevidense																		
1095	EUPH	Sapium	obovatum																		
1096	EUPH	Sebastiania	catingae																		
1097	KRAM	Krameria	tomentosa																		
1098	LEGC	Bauhinia	acuruana																		
1099	LEGC	Bauhinia	cacovia ssp blanchetiana																		
1100	LEGC	Bauhinia	catingae																		
1101	LEGC	Bauhinia	cheilantha																		
1102	LEGC	Bauhinia	dumosa																		
1103	LEGC	Bauhinia	estivana																		
1104	LEGC	Bauhinia	flexuosa																		
1105	LEGC	Bauhinia	pentandra																		
1106	LEGC	Caesalpinia	bracteosa																		
1107	LEGC	Caesalpinia	calycina																		
1108	LEGC	Caesalpinia	ferrea																		
1109	LEGC	Caesalpinia	gardneriana																		
1110	LEGC	Caesalpinia	laxiflora																		
1111	LEGC	Caesalpinia	microphylla																		
1112	LEGC	Caesalpinia	pyramidalys																		
1113	LEGC	Cenostigma	gardneriana																		
1114	LEGC	Cenostigma	macrophyllum																		
1115	LEGC	Chamaecrista	acosmifolia																		
1116	LEGC	Chamaecrista	amiciella																		
1117	LEGC	Chamaecrista	barbata																		
1118	LEGC	Chamaecrista	belemii																		
1119	LEGC	Chamaecrista	carobinha																		
1120	LEGC	Chamaecrista	desvauxii v latifolia																		
1121	LEGC	Chamaecrista	pascuorum																		
1122	LEGC	Chamaecrista	rotundifolia v rotundifolia																		
1123	LEGC	Chamaecrista	supplex																		
1124	LEGC	Chamaecrista	zygophylloides																		
1125	LEGC	Copaifera	coriacea																		
1126	LEGC	Copaifera	luetzelburgii																		
1127	LEGC	Copaifera	martii																		
1128	LEGC	Diptychandra	aurantiaca ssp. epunctata																		
1129	LEGC	Goniorrhachis	marginata																		
1130	LEGC	Hymenaea	eriogyne																		
1131	LEGC	Hymenaea	martiana																		
1132	LEGC	Hymenaea	velutina																		
1133	LEGC	Martiodendron	mediterraneum																		
1134	LEGC	Peltogyne	paucifiora																		
1135	LEGC	Poeppigia	procera																		
1136	LEGC	Senna	acuruensis																		
1137	LEGC	Senna	aversiflora																		
1138	LEGC	Senna	gardneri																		
1139	LEGC	Senna	harleyi																		
1140	LEGC	Senna	macranthera																		
1141	LEGC	Senna	martiana																		
1142	LEGC	Senna	rizzinii																		
1143	LEGC	Senna	splendida v.gloriosa																		
1144	LEGC	Senna	uniflora																		
1145	LEGM	Acacia	bahiensis																		
1146	LEGM	Acacia	farnesiana																		
1147	LEGM	Acacia	langsdorffii																		
1148	LEGM	Acacia	martii																		
1149	LEGM	Acacia	piauhiensis																		
1150	LEGM	Acacia	riparia																		

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				MONSCh	CHAAUT	SeHGalI	AURIPLA	PabIICAA	CALGJAN	VENMCOL	ECU	CER	PIAEAM2								
1151	LEGM	Albizia	blanchetii																		
1152	LEGM	Albizia	polycephala																		
1153	LEGM	Calliandra	depauperata																		
1154	LEGM	Calliandra	leptopoda																		
1155	LEGM	Calliandra	macrocalyx																		
1156	LEGM	Calliandra	squarrosa																		
1157	LEGM	Chloroleucon	dumosum																		
1158	LEGM	Chloroleucon	foliolosum																		
1159	LEGM	Mimosa	acutistipula																		
1160	LEGM	Mimosa	adenophylla																		
1161	LEGM	Mimosa	campicola v. planipes																		
1162	LEGM	Mimosa	caesalpiniifolia																		
1163	LEGM	Mimosa	coruscocaesia																		
1164	LEGM	Mimosa	exalbescens																		
1165	LEGM	Mimosa	gemmulata v.gemmulata																		
1166	LEGM	Mimosa	glaucula																		
1167	LEGM	Mimosa	hexandra																		
1168	LEGM	Mimosa	invisa																		
1169	LEGM	Mimosa	irrigua																		
1170	LEGM	Mimosa	misera																		
1171	LEGM	Mimosa	modesta																		
1172	LEGM	Mimosa	morroensis																		
1173	LEGM	Mimosa	nothopteris																		
1174	LEGM	Mimosa	ophtalmocentra																		
1175	LEGM	Mimosa	paludosa																		
1176	LEGM	Mimosa	pseudoseptaria																		
1177	LEGM	Mimosa	ulbrichiana																		
1178	LEGM	Mimosa	ursina																		
1179	LEGM	Mimosa	verrucosa																		
1180	LEGM	Mimosa	xiquexiquensis																		
1181	LEGM	Paraptadenia	blanchetii																		
1182	LEGM	Paraptadenia	zehntneri																		
1183	LEGM	Piptadenia	moniliformes																		
1184	LEGM	Piptadenia	obliqua																		
1185	LEGM	Piptadenia	stipulacea																		
1186	LEGM	Pithecellobium	diversifolium																		
1187	LEGM	Stryphnodendron	cortaceum																		
1188	LEGM	Stryphnodendron	piptadenioides																		
1189	LEGP	Acosmium	fallax																		
1190	LEGP	Aeschynomene	filosa																		
1191	LEGP	Aeschynomene	martii																		
1192	LEGP	Bocoa	mollis																		
1193	LEGP	Calopogonium	velutinum																		
1194	LEGP	Canavalia	dictyota																		
1195	LEGP	Coursetia	rostrata																		
1196	LEGP	Coursetia	vicioides																		
1197	LEGP	Cratylia	mollis																		
1198	LEGP	Cratylia	nuda																		
1199	LEGP	Dalbergia	catingicola																		
1200	LEGP	Dalbergia	cearensis																		
1201	LEGP	Dalbergia	decipularis																		
1202	LEGP	Dalbergia	glaucescens																		
1203	LEGP	Dioclea	glabra																		
1204	LEGP	Dioclea	grandiflora																		
1205	LEGP	Dioclea	guianensis v.lasiophylla																		
1206	LEGP	Discolobium	hirtum																		
1207	LEGP	Lonchocarpus	araripensis																		
1208	LEGP	Lonchocarpus	campestris																		
1209	LEGP	Lonchocarpus	sericeus																		
1210	LEGP	Lonchocarpus	virgilioides																		
1211	LEGP	Luetzelburgia	andrade-limae																		
1212	LEGP	Luetzelburgia	auriculata																		
1213	LEGP	Luetzelburgia	bahiensis																		
1214	LEGP	Machaerium	angustifolium																		
1215	LEGP	Machaerium	leucopterum																		
1216	LEGP	Machaerium	punctatum																		
1217	LEGP	Platymiscium	obtusifolium																		
1218	LEGP	Platymiscium	zehntneri																		
1219	LEGP	Poecilanthe	falcata																		
1220	LEGP	Poecilanthe	subcordata																		
1221	LEGP	Poecilanthe	ulei																		
1222	LEGP	Pterocarpus	ternatus																		
1223	LEGP	Pterocarpus	villosus																		
1224	LEGP	Pterocarpus	zehntneri																		
1225	LEGP	Riedeliella	graciliflora																		
1226	LEGP	Riedeliella	magalhaesii																		
1227	LEGP	Swartzia	apetala v.apetala																		
1228	LEGP	Zollernia	ilicifolia																		
1229	MALP	Dicella	bracteosa																		
1230	MALP	Heteropterys	trichanthera																		
1231	MALP	Stigmatophyllon	auriculatum																		
1232	MALV	Gaya	gaudichaudiana																		
1233	MALV	Gaya	aurea																		
1234	MALV	Herissantia	crispa																		
1235	MALV	Herissantia	tiubae																		
1236	MALV	Pavonia	andrade-limae																		
1237	MALV	Pavonia	humifussa																		
1238	MALV	Pavonia	martii																		
1239	MALV	Sida	galheirensis																		
1240	MALV	Sida	micrantha																		
1241	MALV	Wissadula	contracta																		
1242	MALV	Wissadula	patens																		
1243	MORA	Brosimum	gaudichaudii																		
1244	MYRT	Campomanesia	eugenioides v.deserterum																		
1245	NYCT	Bougainvillea	glabra																		
1246	NYCT	Pisonia	tomentosa																		
1247	OLAC	Schoepfia	brasiliensis																		
1248	OLAC	Ximenia	cortacea																		
1249	POLY	Triplaris	gardneriana																		
1250	RHAM	Alvimiantha	tricamerata																		

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				MONSCh	CHAAUT	SeHGalI	AURIPLA	PabIICAA	CALGJAN	VENMCOL	ECU	CER	PIAEAM2								
1251	RHAM	Ziziphus	cotinifolia																		
1252	RHAM	Ziziphus	joazeiro																		
1253	RUBI	Alseis	involuta																		
1254	RUBI	Coccocypselum	dichroolasium																		
1255	RUBI	Guettarda	angelica																		
1256	RUBI	Machaonia	spinosa																		
1257	RUBI	Simira	sp.																		
1258	SAPI	Serjania	comata																		
1259	SOLA	Brunfelsia	clandestina																		
1260	SOLA	Solanum	chaetacanthum																		
1261	STER	Ayenia	blanchetiana																		
1262	STER	Ayenia	erecta																		
1263	STER	Ayenia	hirta																		
1264	STER	Helicteres	eichleri																		
1265	STER	Helicteres	mollis																		
1266	STER	Helicteres	velutina																		
1267	STER	Melochia	betonicifolia																		
1268	STER	Waltheria	ferruginea																		
1269	ULMA	Phyllostylon	brasiliense																		
1270	VELL	Xerophyta	cinerascens																		
1271	VELL	Xerophyta	plicata																		
1272	VERB	Amasonia	campestris																		
1273	VERB	Lantana	caatingensis																		
1274	VERB	Lantana	camara																		
1275	VERB	Lippia	bahiensis																		
1276	VERB	Lippia	gracilis																		
1277	VERB	Stachytarpheta	sanguinea																		
1278	VERB	Vitex	gardneriana																		
1279	VITA	Cissus	coccinea																		
1280	VITA	Cissus	simsiana																		
1281	LEGP	Machaerium	hirtum																		
1282	BOMB	Pseudobombax	sp.																		
1283	AREC	Acrocomia	total																		
1284	STER	Helicteres	lhotskyana																		
1285	EUPH	Croton	spl																		
1286	BIGN	Jacaranda	sp.																		
1287	CAPP	Capparis	mattogrossensis																		
1288	ERYT	Erythroxylum	sp.																		
1289	LEGP	Acosmium	cardenasii																		
1290	LEGP	Erythrina	verna																		
1291	LEGP	Lonchocarpus	sp.																		
1292	LEGM	Anadenanthera	sp.? ('angico preto')																		
1293	NYCT	Pisonia	sp.																		
1294	POLY	Coccoloba	sp.																		
1295	RUBI	Simira	corumbensis?																		
1296	RUTA	Metrodorea	mollis																		
1297	TILI	Luehea	sp.																		
1298	VERB	Vitex	cymosa																		
1299	ANAC	Schinus	spp																		
1300	BIGN	Tabebuia	sp?																		
1301	CARI	Carica	sp?																		
1302	CELA	Maytenus	horrida																		
1303	COMB	Combretum	duarteanum																		
1304	EUPH	Jatropha	sp.('serinquarana')																		
1305	LEGC	Bauhinia	platysepala?																		
1306	LEGP	Machaerium	spl ('cupiuba')																		
1307	LEGP	Machaerium	spll ('concileiro branco')																		
1308	LEGM	Acacia	claussenii?																		
1309	LEGM	Calliandra	myriophylla																		
1310	POLY	Triplaris	sp. ('pau Jau')																		
1311	RUTA	Fagara	sp.																		
1312	SAPI	Dilodendron	bipinnatum																		
1313	SAPO	Pouteria	sp. ('cuquirina')																		
1314	STER	Helicteres	sp.																		
1315	VERB	Vitex	sp. ('Tarumã')																		
1316	VOCH	Callisthene	fasciculata																		
1317	ACAN	Bravaisia	integerrima																		
1318	ANNO	Annona	jahnii																		
1319	APOC	Rauvolfia	tetraphylla																		
1320	ARAL	Sciadodendron	excelsum																		
1321	BIGN	Godmania	aesculifolia																		
1322	BORA	Beureria	cumanensis																		
1323	BORA	Cordia	collococca																		
1324	BORA	Cordia	umbellifera																		
1325	BORA	Rochefortia	spinosa																		
1326	BROM	Bromelia	chrysantha																		
1327	BURS	Bursera	sp.																		
1328	CACT	Acanthocereus	pentagonus																		
1329	CACT	Opuntia	sp.																		
1330	CAPP	Capparis	verrucosa																		
1331	CHRY	Licania	pyrifolia																		
1332	ERYT	Erythroxylum	cumanense																		
1333	EUPH	Sapium	sp.																		
1334	LECY	Lecythis	ollaria																		
1335	LEGM	Acacia	striata																		
1336	LEGM	Acacia	tamarindifolia																		
1337	LEGM	Acacia	sp.																		
1338	LEGM	Calliandra	affinis																		
1339	LEGM	Enterolobium	cyclocarpum																		
1340	LEGM	Albizia	corymbosa																		
1341	LEGM	Pithecellobium	carabobense																		
1342	LEGM	Pithecellobium	ligustrinum																		
1343	LEGC	Bauhinia	aculeata																		
1344	LEGC	Caesalpinia	granadillo																		
1345	LEGP	Centrolobium	paraense																		
1346	LEGP	Fissicalyx	fendleri																		
1347	LEGP	Lonchocarpus	dipteroneurus																		
1348	LEGP	Lonchocarpus	ernestii																		
1349	LEGP	Lonchocarpus	lutescens																		
1350	LEGP	Lonchocarpus	sp.tua																		

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				HONSC	HCHA	AUT	SENSA	IT	AURIPLA		Pabl	ICAA	CALQ	JAN	IVEN	COL	ECU	CER	MAT	TUMZ	
1351	LEGP	Lonchocarpus	sp.																		
1352	LEGP	Machaerium	amplum																		
1353	LEGP	Machaerium	grandifolium																		
1354	LEGP	Machaerium	sp.																		
1355	LEGP	Piscidia	quaricensis																		
1356	LEGP	Mucuna	aterrimum																		
1357	LOGA	Strychnos	fendleri																		
1358	MALP	Banisteria	cornifolia																		
1359	MALP	Bunchosia	sp.																		
1360	MELI	Trichilia	palmetorum																		
1361	MELI	Trichilia	unifoliola																		
1362	MELI	Trichilia	sp.																		
1363	MORA	Ficus	sp.																		
1364	MYRT	Myrcia	sp.																		
1365	NYCT	Pisonia	ferruginea																		
1366	OCHN	Ouratea	grossourdi																		
1367	AREC	Copernicia	tectorum																		
1368	AREC	Bactris	sp.																		
1369	POLG	Bredemeyera	sp.																		
1370	POLY	Coccoloba	caracasana																		
1371	POLY	Coccoloba	sp.																		
1372	RUBI	Alseis	labatioides																		
1373	RUBI	Genipa	caruto																		
1374	RUBI	Randia	dioica																		
1375	RUTA	Fagara	spp.																		
1376	RUTA	Zanthoxylum	syncarpum																		
1377	SAPI	Allophylus	occidentalis																		
1378	SAPI	Melicoca	bijuga																		
1379	SAPI	Talisia	sp.																		
1380	SOLA	Brunfelsia	sp.																		
1381	STER	Sterculia	apetala																		
1382	TILI	Apeiba	tibourbou																		
1383	ULMA	Celtis	sp.																		
1384	VERB	Aegiphila	sp.																		
1385	VERB	Vitex	appuni																		
1386	VERB	Vitex	sp.																		
1387	ZYGO	Bulnesia	arborea																		
1388	EUPH	Jatropha	gossypifolia																		
1389	EUPH	Phyllanthus	botryanthus																		
1390	CACT	Stenocereus	(Ritterocereus?) spp.																		
1391	CACT	Cephalocereus	moritzianus																		
1392	LEGC	Bauhinia	guianensis																		
1393	LEGP	Platymiscium	dladelphum																		
1394	LEGP	Apoptanesia	cryptopetala																		
1395	RUTA	Pilocarpus	spp.																		
1396	RUTA	Helietta	pleeana																		
1397	RUTA	Zanthoxylum	monophyllum																		
1398	APOC	Plumeria	pudica																		
1399	CELA	Maytenus	spp.																		
1400	NYCT	Pisonia	spp.																		
1401	MYRT	Eugenia	spp.																		
1402	SAPI	Paullinia	pinnata																		
1403	EUPH	Croton	hellaster																		
1404	LEGM	Pithecellobium	unguis-cati																		
1405	LEGM	Calliandra	tergemina																		
1406	LEGP	Lonchocarpus	atropurpureus																		
1407	THEO	Jacquinia	caracasana																		
1408	BURS	Bursera	karstenlana																		
1409	FLAC	Casearia	zyzyphoides																		
1410	RUBI	Machaonia	ottonis																		
1411	POLY	Ruprechtia	sp.																		
1412	FLAC	Zueilania	roussoviae																		
1413	MELI	Trichilia	trifolia																		
1414	VITA	Cissus	trifoliata																		
1415	CACT	Opuntia	wentiana																		
1416	CACT	Cereus	margaritensis																		
1417	LEGC	Bauhinia	glabra																		
1418	RUTA	Amyris	silvatica																		
1419	APOC	Plumeria	inodora																		
1420	CELA	Pristimera	verrucosa																		
1421	CELA	Schaefferia	frutescens																		
1422	CELA	Hippocratea	volubilis																		
1423	NYCT	Pisonia	inermis																		
1424	MYRT	Eugenia	umbellifera																		
1425	SAPI	Paullinia	cururu																		
1426	SAPI	Serjania	colombiana																		
1427	EUPH	Croton	populifolius																		
1428	EUPH	Croton	guildingii																		
1429	EUPH	Croton	malambo																		
1430	EUPH	Croton	niveus																		
1431	MALP	Banisteria	heterostyla																		
1432	MALP	Bunchosia	odorata																		
1433	LEGM	Pithecellobium	pubescens																		
1434	LEGM	Acacia	costaricense																		
1435	LEGM	Calliandra	magdalenae																		
1436	LEGM	Piptadenia	flava																		
1437	LEGP	Lonchocarpus	sanctae-martae																		
1438	LEGP	Coursetia	caribaea																		
1439	LEGP	Gliricidia	sepium																		
1440	LEGP	Machaerium	glabratum																		
1441	THEO	Jacquinia	aristata																		
1442	BURS	Bursera	gummifera																		
1443	BURS	Bursera	glabra																		
1444	POLY	Coccoloba	obtusifolia																		
1445	POLY	Coccoloba	cerenata																		
1446	POLY	Triplaris	purdiei																		
1447	STER	Ayenia	magna																		
1448	BIGN	Arrabidea	pleei																		
1449	CONV	Ipomoea	trifida																		
1450	BORA	Cordia	sydneyensis																		

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				HONSC	HCHA	AUT	SENSA	IT	AURIPLA		Pabl	ICAA	CALQ	JAN	IVEN	COL	ECU	CER	MAT	TUMZ	
1451	APOC	Rauvolfia	ligustrina																		
1452	APOC	Stemmadenia	grandiflora																		
1453	LEGC	Caesalpinia	punctata																		
1454	LECY	Lecythis	minor																		
1455	ERYT	Erythroxylum	havanense																		
1456	ASTE	Lycoseris	crocata																		
1457	OCHN	Ouratea	guildingii																		
1458	SMIL	Smilax	spinosa																		
1459	VERB	Lippia	americana																		
1460	SOLA	Cestrum	alternifolium																		
1461	BIGN	Arrabidea	mollissima																		
1462	BIGN	Anemopægna	orbiculatum																		
1463	BIGN	Clytostoma	cuneatum																		
1464	BIGN	Crescentia	cujete																		
1465	BIGN	Xylophragma	seemannlana																		
1466	MALP	Heteropterys	formosa																		
1467	MALP	Heteropterys	rhombifolia																		
1468	MALP	Hiraea	reclinata																		
1469	ASCL	Marsdenia	xerophylica																		
1470	ASCL	Matelea	maritima																		
1471	ANAC	Loxopterigium	huasango																		
1472	RHAM	Ziziphus	thyrsiflora																		
1473	BORA	Cordia	lutea																		
1474	THEO	Jacquinia	pubescens																		
1475	THEO	Clavija	pungens																		
1476	CACT	Armatocereus	cartwrightianus																		
1477	CACT	Opuntia	sp.																		
1478	CACT	Hylocereus	peruvianus																		
1479	LEGC	Caesalpinia	corymbosa																		
1480	LEGC	Senna	reticulata																		
1481	LEGC	Senna	hartwegi																		
1482	LEGC	Senna	incarnata																		
1483	LEGP	Aeschynomene	platycarpa																		
1484	LEGM	Leucaena	canescens																		
1485	LEGM	Leucaena	trichodes																		
1486	LEGM	Prosopis	pallida																		
1487	BROM	Bromelia	pinguin																		
1488	EUPH	Croton	rivinifolius																		
1489	EUPH	Croton	sp.																		
1490	EUPH	Acalypha	wilkesiana																		
1491	VERB	Lantana	moritziana																		
1492	CAPP	Capparis	avicennifolia																		
1493	CAPP	Capparis	scabrida																		
1494	CAPP	Capparis	crotonoides																		
1495	ANAC	Spondias	purpurea																		
1496	ANAC	Anacardium	occidentale																		
1497	APOC	Rauvolfia	heterophylla																		
1498	ERYT	Erythroxylum	glaucum																		
1499	ARAL	Nothopanax	ornatus																		
1500	CARI	Carica	parviflora																		
1501	STER	Waltheria	ovata																		
1502	ASTE	Wedelia	grandiflora																		
1503	BOMB	Ceiba	trichistandra																		
1504	BOMB	Cavanillesia	platanifolia																		
1505	BOMB	Eriotheca	ruizii																		
1506	BOMB	Pseudobombax	millei																		
1507	BOMB	Pseudobombax	guayasense																		
1508	LEGM	Mimosa	albida																		
1509	BIGN	Tecoma	castanifolia																		
1510	ACHA	Achatocarpus	pubescens																		
1511	ANNO	Annona	crassiflora																		
1512	ANNO	Guatteria	sellowiana																		
1513	ANNO	Xilopia	aromatica																		
1514	ANNO	Xilopia	sericea																		
1515	APOC	Aspidosperma	macrocarpon																		
1516	APOC	Hancornia	pubescens																		
1517	AQUI	Ilex	conocarpa																		
1518	ARAL	Didymopanax	macrocarpum																		
1519	AREC	Syagrus	flexuosa																		
1520	AREC	Butia	leiospatha																		
1521	BOMB	Eriotheca	pubescens																		
1522	BOMB	Pseudobombax	longiflorum																		
1523	BOMB	Pseudobombax	tomentosum																		
1524	CARY	Caryocar	brasiliensis																		
1525	CELA	Austroplenckia	populnea																		
1526	CELA	Cheliocthnum	cognatum																		
1527	CELA	Salacia	crassifolia																		
1528	CHRY	Couepia	grandiflora																		
1529	CHRY	Hirtella	glandulosa																		
1530	CHRY	Licania	humilis																		
1531	CLUS	Kielmeyera	coriacea																		
1532	CLUS	Kielmeyera	speciosa																		
1533	COMB	Terminalia	argentea																		
1534	ASTE	Eremanthus	glomerulatus																		
1535	ASTE	Eremanthus	goyazensis																		
1536	ASTE	Gochnatia	sp.																		
1537	ASTE	Piptocarpha	rotundifolia																		
1538	ASTE	Vernonia	ferruginea																		
1539	CONN	Connarus	suberosus																		
1540	CONN	Rourea	induta																		
1541	DILL	Davilla	elliptica																		
1542	EBEN	Diospyros	burchellii																		
1543	ERYT	Erythroxylum	suberosum																		
1544	ERYT	Erythroxylum	tortuosum																		
1545	FLAC	Casearia	grandiflora																		
1546	ICAC	Emmotum	nitens																		
1547	LAUR	Ocotea	spixiana																		
1548	LAUR	Phoebe	erythrobus																		
1549	LEGC	Dimorphandra	mollis																		
1550	LEGC	Hymenaea	stigonocarpa																		

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				MONSO	SOL	CHA	AUT	SE	NGA	ILL	AUR	PLA	Pas	ICA	AA	CAL	QUA	JAN	VEN	COL	ECU	CER	MAT	LAM	2
1551	LEGC	Sclerolobium	aureum																						
1552	LEGC	Sclerolobium	paniculatum																						
1553	LEGM	Enterolobium	ellipticum																						
1554	LEGM	Mimosa	claussenii																						
1555	LEGM	Plathymenia	reticulata																						
1556	LEGM	Stryphnodendron	adstringens																						
1557	LEGP	Andira	paniculata																						
1558	LEGP	Bowdichia	virgilioides																						
1559	LEGP	Machaerium	opacum																						
1560	LEGP	Platypodium	grandiflorum																						
1561	LEGP	Pterodon	emarginatus																						
1562	LEGP	Vatairea	macrocarpa																						
1563	LOGA	Antonia	ovata																						
1564	LOGA	Strychnos	pseudoquina																						
1565	LYTH	Lafoensia	pacari																						
1566	MALP	Banisteria	latifolia																						
1567	MALP	Byrsonima	coccolobifolia																						
1568	MALP	Byrsonima	crassa																						
1569	MALP	Byrsonima	laxiflora																						
1570	MALP	Byrsonima	verbascifolia																						
1571	MALP	Heteropterys	byrsonimifolia																						
1572	MELA	Miconia	albicans																						
1573	MELA	Miconia	burchellii																						
1574	MELA	Miconia	cuspidata																						
1575	MELA	Miconia	ferruginata																						
1576	MELA	Miconia	pohliana																						
1577	MELA	Miconia	rubiginosa																						
1578	MELA	Miconia	sellowiana																						
1579	MYRI	Virola	sebifera																						
1580	MYRS	Rapanea	guianensis																						
1581	MYRS	Cybianthus	detergens																						
1582	MYRT	Blepharocalyx	salicifolius																						
1583	MYRT	Eugenia	dysenterica																						
1584	MYRT	Eugenia	pileolis																						
1585	MYRT	Gomidesia	brunei																						
1586	MYRT	Pimenta	pseudocaryophyllus																						
1587	MYRT	Psidium	myrsinoides																						
1588	MYRT	Psidium	warmingianum																						
1589	MYRT	Siphoneugena	densiflora																						
1590	MYRT	Myrcia	variabilis																						
1591	NYCT	Neea	theifera																						
1592	NYCT	Pisonia	noxia																						
1593	NYCT	Pisonia	gracilliflora																						
1594	NYCT	Pisonia	sp.																						
1595	OCHN	Ouratea	hexasperma																						
1596	PROT	Roupala	montana																						
1597	ROSA	Prunus	brasiliensis																						
1598	RUBI	Alibertia	edulis																						
1599	RUBI	Ferdinandusa	elliptica																						
1600	RUBI	Palicourea	rigida																						
1601	RUBI	Tocoyena	formosa																						
1602	SAPO	Pouteria	ramiflora																						
1603	SAPO	Pouteria	torta																						
1604	SIMA	Simarouba	versicolor																						
1605	SOLA	Solanum	lycocarpum																						
1606	STYR	Styrax	ferrugineus																						
1607	SYMP	Symplocos	rhamnifolia																						
1608	TILI	Luehea	paniculata																						
1609	VELL	Vellozia	squamata																						
1610	VERB	Aegiphila	lhotskyana																						
1611	VOCH	Callisthene	major																						
1612	VOCH	Qualea	grandiflora																						
1613	VOCH	Qualea	parviflora																						
1614	VOCH	Salvertia	convallariodora																						
1615	VOCH	Vochysia	elliptica																						
1616	VOCH	Vochysia	rufa																						
1617	VOCH	Vochysia	thyrsoidea																						
1618	VOCH	Vochysia	tucanorum																						
1619	ANAC	Tapirira	guianensis																						
1620	ANNO	Anaxagorea	dolichopetala																						
1621	ANNO	Guatteria	nigrescens																						
1622	ANNO	Xilopia	brasiliensis																						
1623	APOC	Aspidosperma	compactinervium																						
1624	APOC	Malouetia	arborea																						
1625	AQUI	Ilex	dumosa																						
1626	AQUI	Ilex	theezans																						
1627	ARAL	Didimopanax	calvum																						
1628	AREC	Astrocaryum	aculeatissimum																						
1629	AREC	Attalea	dubia																						
1630	AREC	Barbosa	pseudococos																						
1631	ASTE	Stiftia	graziellii																						
1632	ASTE	Vernonia	discolor																						
1633	BIGN	Tabebuia	cassinoides																						
1634	BOMB	Eriotheca	pentaphylla s.wittrockiana																						
1635	BOMB	Eriotheca	sp.																						
1636	BORA	Cordia	sellowiana																						
1637	CHRY	Hirtella	hebeclada																						
1638	CHRY	Hirtella	sp.																						
1639	CHRY	Licania	kunthiana																						
1640	CHRY	Licania	riedelii																						
1641	CLET	Clethra	scabra v. laevigata																						
1642	CLUS	Rheedia	brasiliensis																						
1643	COMB	Terminalia	januariensis																						
1644	CUNO	Lamanonia	glabra																						
1645	ERYT	Erythroxylum	pulchrum																						
1646	EUPH	Asanthmium	cordatum																						
1647	EUPH	Hyeronima	alchorneoides																						
1648	EUPH	Mabea	brasiliensis																						
1649	EUPH	Pera	leandri																						
1650	LACI	Lacistema	ellipticum																						

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				MONSO	SOL	CHA	AUT	SE	NGA	ILL	AUR	PLA	Pas	ICA	AA	CAL	QUA	JAN	VEN	COL	ECU	CER	MAT	LAM	2
1651	LAUR	Aniba	firmula																						
1652	LAUR	Ocotea	brachybotra																						
1653	LAUR	Ocotea	porosa																						
1654	LAUR	Ocotea	silvestris																						
1655	LAUR	Ocotea	teleiandra																						
1656	LAUR	Ocotea	spp.																						
1657	LECY	Lecythis	pisonis																						
1658	LEGC	Sclerolobium	denudatum																						
1659	LEGM	Inga	flagelliformis																						
1660	LEGM	Inga	nutans																						
1661	LEGM	Inga	sp.																						
1662	LEGM	Macrosamanea	pedicellare																						
1663	LEGM	Pseudopiptadenia	leptostachyum																						
1664	LEGP	Hymenolobium	janeirelsence																						
1665	LEGP	Machaerium	vestitum																						
1666	MELA	Henriettella	glaora																						
1667	MELA	Miconia	candolleana																						
1668	MELA	Miconia	chartana																						
1669	MELA	Miconia	sp.																						
1670	MELI	Trichilia	silvatica																						
1671	MONI	Mollinedia	triflora																						
1672	CECR	Cecropia	glaziovi																						
1673	MORA	Ficus	gomelleira																						
1674	MORA	Pourouma	acutifolia																						
1675	MYRI	Virola	gardneri																						
1676	MYRI	Virola	oleifera																						
1677	MYRT	Calycorectes	acutifolia																						
1678	MYRT	Calyptranthes	spp.																						
1679	MYRT	Eugenia	cerasiflora																						
1680	MYRT	Gomidesia	anacardiaefolia																						
1681	MYRT	Marlierea	glaora																						
1682	MYRT	Marlierea	obscura																						
1683	MYRT	Marlierea	parviflora																						
1684	MYRT	Marlierea	silvatica																						
1685	MYRT	Marlierea	suaveolens																						
1686	MYRT	Marlierea	tomentosa																						
1687	MYRT	Marlierea	sp.																						
1688	MYRT	Myrcia	pubipetala																						
1689	MYRT	Myrcia	sp.																						
1690	NYCT	Pisonia	calycantha																						
1691	OLAC	Heisteria	silvanii																						
1692	PROT	Euplassa	cantareirae																						
1693	PROT	Roupala	lucens																						
1694	PROT	Roupala	sp.																						
1695	ROSA	Prunus	sphaerocarpa																						
1696	RUBI	Amaioua	guianensis																						
1697	RUBI	Bathysa	australis																						
1698	RUBI	Bathysa	gymnocarpa																						
1699	RUBI	Coussarea	meridionalis																						
1700	RUBI	Coussarea	nodosa																						
1701	RUBI	Coussarea	porophylla																						
1702	RUBI	Psychotria	hancorniifolia																						
1703	SAPI	Cupania	oblongifolia																						
1704	SAPI	Cupania	racemosa																						
1705	SAPI	Matayba	guianensis																						
1706	SAPO	Chrysophyllum	flexuosum																						
1707	SAPO	Ecclinusa	ramiflora																						
1708	SAPO	Micropholis	sp.																						
1709	SAPO	Pouteria	sp.																						
1710	SAPO	Micropholis	gardneriana																						
1711	SYMP	Symplocos	celastrinea																						
1712	VOCH	Qualea	gestasiana																						
1713	VOCH	Vochysia	acuminata s.laurifolia																						
1714	ANNO	Anaxagorea	phaeocarpa																						
1715	ANNO	Annona	sp.																						
1716	ANNO	Bocageopsis	multiflora																						
1717	ANNO	Bocageopsis	matogrossensis																						
1718	ANNO	Duguetia	caudata																						
1719	ANNO	Duguetia	flagellaris																						
1720	ANNO	Ephedranthus	amazonicus																						
1721	ANNO	Guatteria	olivacea																						
1722	ANNO	Unonopsis	duckei																						
1723	ANNO	Unonopsis	stipitata																						
1724	ANNO	Unonopsis	sp.																						
1725	APOC	Ambelania	duckei																						
1726	APOC	Anacampta	rigida																						
1727	APOC	Aspidosperma	album																						
1728	APOC	Geissospermum	argenteum																						
1729	APOC	Peschiera	disticha																						
1730	APOC	Peschiera	macrophylla																						
1731	AREC	Oenocarpus	bacaba																						
1732	AREC	Oenocarpus	minor																						
1733	AREC	Syagrus	sp.																						
1734	BOMB	Bombacopsis	nervosa																						
1735	BOMB	Scleronema	micranthum																						
1736	BURS	Protium	apiculatum																						
1737	BURS	Protium	heptaphyllum																						
1738	BURS	Protium	insigne																						
1739	BURS	Protium	opacum																						
1740	BURS	Protium	paraense																						
1741	BURS	Protium	pedicellatum																						
1742	BURS	Protium	sagotianum																						
1743	BURS	Protium	sp.																						
1744	BURS	Tetragastris	altissima																						
1745	BURS	Tetragastris	panamensis																						
1746	BURS	Tetragastris	trifoliolata																						
1747	BURS	Tetragastris	sp.																						
1748	CARY	Caryocar	pallidum																						
1749	CELA	Salacia	impressifolia																						
1750	CELA	Salacia	sp.																						

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				MON	SCH	CHA	AUT	SEN	GAI	AUR	PLA	Pab	CAA	CAL	JAN	VEN	COL	ECU	CER	MAT	AMZ
1751	CHRY	Couepia	obovata																		
1752	CHRY	Couepia	canomensis																		
1753	CHRY	Hirtella	bicornis																		
1754	CHRY	Licania	caudata																		
1755	CHRY	Licania	hypoleuca																		
1756	CHRY	Licania	longistyla																		
1757	CHRY	Licania	micrantha																		
1758	CHRY	Licania	octandra																		
1759	CHRY	Licania	pallida																		
1760	CHRY	Licania	heteromorpha																		
1761	CLUS	Tovomita	sp																		
1762	CHRY	Parinari	excelsa																		
1763	COMB	Buchenavia	sp.																		
1764	CONN	Rourea	sp																		
1765	DICH	Tapura	guianensis																		
1766	DUCK	Duckeodendron	cestroides																		
1767	ELAE	Sloanea	floribunda																		
1768	ELAE	Sloanea	laurifolia																		
1769	EUPH	Conceveiba	guianensis																		
1770	EUPH	Croton	sp.																		
1771	EUPH	Pera	schomburgkiana																		
1772	EUPH	Pogonophora	schomburgkiana																		
1773	FLAC	Casearia	aculeata																		
1774	FLAC	Casearia	javitensis																		
1775	FLAC	Laetia	procera																		
1776	GNET	Gnetum	sp.																		
1777	HUMI	Endopleura	uchi																		
1778	HUMI	Saccoglottis	ceratocarpa																		
1779	HUMI	Saccoglottis	matogrossensis																		
1780	LAUR	Aniba	duckei																		
1781	LAUR	Aniba	guianensis																		
1782	LAUR	Aniba	sp.																		
1783	LAUR	Licaria	aurea																		
1784	LAUR	Licaria	aritu																		
1785	LAUR	Licaria	sp.																		
1786	LAUR	Ocotea	neesiana																		
1787	LAUR	Nectandra	rubra																		
1788	LECY	Corythophora	alta																		
1789	LECY	Corythophora	rimosa																		
1790	LECY	Couratari	guianensis																		
1791	LECY	Couratari	tauari																		
1792	LECY	Eschweilera	amara																		
1793	LECY	Eschweilera	fracta																		
1794	LECY	Eschweilera	odora																		
1795	LECY	Eschweilera	polyantha																		
1796	LECY	Eschweilera	spp.																		
1797	LECY	Holopyxidium	latifolium																		
1798	LECY	Holopyxidium	jaranum																		
1799	LECY	Holopyxidium	spp.																		
1800	LEGP	Bocoa	alterna																		
1801	LEGC	Eperua	bijuga																		
1802	LEGC	Macrolobium	unijugum																		
1803	LEGC	Macrolobium	sp.																		
1804	LEGC	Peltogyne	paniculata																		
1805	LEGP	Swartzia	cuspidata																		
1806	LEGP	Swartzia	corrugata																		
1807	LEGP	Swartzia	panacoco																		
1808	LEGP	Swartzia	reticulata																		
1809	LEGP	Swartzia	spp.																		
1810	LEGM	Inga	bullatorugosa																		
1811	LEGM	Inga	glomeriflora																		
1812	LEGM	Inga	laeglfera																		
1813	LEGM	Inga	myriantha																		
1814	LEGM	Inga	rubiginosa																		
1815	LEGM	Inga	sp.																		
1816	LEGM	Piptadenia	sp.																		
1817	LEGM	Pithecellobium	racemosum																		
1818	LEGM	Stryphnodendron	racemiferum																		
1819	LEGP	Andira	unifoliolata																		
1820	LEGP	Dalbergia	atropurpurea																		
1821	LEGP	Dalbergia	sp																		
1822	LEGP	Dipteryx	odorata																		
1823	MELA	Miconia	elaeagnoides																		
1824	MELA	Miconia	longispicata																		
1825	MELA	Miconia	pyrifolia																		
1826	MELA	Miconia	sp.																		
1827	MELA	Mouriria	angustata																		
1828	MELA	Mouriria	lunatanthera																		
1829	MELA	Mouriria	torquata																		
1830	MELA	Mouriria	sp.																		
1831	MELI	Guarea	duckei																		
1832	MELI	Guarea	subsessiliflora																		
1833	MELI	Guarea	sp																		
1834	MELI	Trichilia	micrantha																		
1835	MELI	Trichilia	sp.																		
1836	MONI	Siparuna	decipiens																		
1837	MONI	Siparuna	sp.																		
1838	MORA	Brosimum	parinarioides																		
1839	MORA	Brosimum	utile																		
1840	MORA	Brosimum	sp.																		
1841	CECR	Cecropia	sp																		
1842	MORA	Ficus	sp.																		
1843	MORA	Helianthostylis	sprucei																		
1844	MORA	Helicostylis	tomentosa																		
1845	MORA	Helicostylis	sp																		
1846	MORA	Maquira	calophylla																		
1847	MORA	Naucleopsis	caloneura																		
1848	MORA	Pourouma	cecropiifolia																		
1849	MORA	Pourouma	mollis																		
1850	MORA	Sorocea	muriculata																		

				A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
				MON	SCH	CHA	AUT	SEN	GAI	AUR	PLA	Pab	CAA	CAL	JAN	VEN	COL	ECU	CER	MAT	AMZ
1851	MORA	Sorocea	sp.																		
1852	MORA	Trimotococcus	amazonicus																		
1853	MYRI	Iryanthera	elliptica																		
1854	MYRI	Iryanthera	laevis																		
1855	MYRI	Virola	calophylla																		
1856	MYRI	Virola	multinervia																		
1857	MYRI	Virola	rufula																		
1858	MYRT	Calyptranthes	sp.																		
1859	MYRT	Eugenia	citrifolia																		
1860	MYRT	Eugenia	egensis																		
1861	MYRT	Eugenia	sp																		
1862	MYRT	Marlierea	umbraticola																		
1863	MYRT	Marlierea	sp.																		
1864	MYRT	Myrcia	citrifolia																		
1865	NYCT	Neea	altissima																		
1866	NYCT	Neea	sp.																		
1867	OCHN	Ouratea	discophora																		
1868	OLAC	Heisteria	sp. 4																		
1869	OLAC	Liriosma	ovata																		
1870	OLAC	Minquartia	guianensis																		
1871	OPIL	Agonandra	sp.																		
1872	QUIN	Quiina	pteridophylla																		
1873	RUBI	Alibertia	sp.																		
1874	RUBI	Chimarrhis	barbata																		
1875	RUBI	Coussarea	sp.																		
1876	RUBI	Duroia	macrophylla																		
1877	RUBI	Faramea	sp.																		
1878	RUBI	Pallcourea	corymbifera																		
1879	RUBI	Rudgea	stipulacea																		
1880	SAPI	Matayba	adenanthera																		
1881	SAPI	Talisia	guianensis																		
1882	SAPI	Talisia	sp																		
1883	SAPO	Ecclinusa	guianensis																		
1884	SAPO	Pouteria	sagotiana																		
1885	SAPO	Pouteria	williamii																		
1886	SAPO	Pouteria	reticulata																		
1887	SAPO	Pouteria	eugenifolia																		
1888	SAPO	Pouteria	sp1																		
1889	SAPO	Pouteria	calm																		
1890	SAPO	Pouteria	guta																		
1891	SAPO	Pouteria	sp.11																		
1892	SAPO	Pouteria	fimbriata																		
1893	SAPO	Chrysophyllum	sp.																		
1894	SAPO	Pouteria	cladantha																		
1895	SAPO	Pouteria	macrophylla																		
1896	SIMA	Simaba	cuspidata																		
1897	STER	Sterculia	pruriens																		
1898	STER	Theobroma	subincana																		
1899	STER	Theobroma	sp.																		
1900	TILI	Lueheopsis	rosea																		
1901	VIOL	Amphirrox	surinamensis																		
1902	VIOL	Leonia	sp.																		
1903	VIOL	Paypayrola	guianensis																		
1904	VIOL	Rinorea	flavescens																		
1905	VIOL	Rinorea	guianensis																		
1906	VIOL	Rinorea	sp.																		
1907	VOCH	Erisma	bicolor																		
1908	VOCH	Erisma	fuscum																		
1909	VOCH	Erisma	sp.																		
1910	VOCH	Qualea	albiflora																		
1911	VOCH	Qualea	brevipedicellata																		
1912	VOCH	Qualea	paraensis																		
1913	VOCH	Qualea	sp.																		
1914	VOCH	Vochysia	vismiaefolia																		

TABLE 6.3: **Phytosociological analysis of the main South American Seasonal Forests. Generic level.**

Column **A**- The Monte province, Argentina (*sensu* Morello, 1958:145-50).

B- Chaco *s.s.*: Sierra Chaco, Argentina (Sayago, 1969, p.224).

C- Chaco *s.s.*: the lowland Chaco in its Eastern, Central and Western districts, Argentina. Floristic list from Sect. 4.1, excluded the species exclusive to the Sierra Chaco.

D- Austro-Brazilian Transitional Forest, Argentina (see Sect. 2.3.3.a). Floristic list from Lewis & Pire, 1981, and author's field experience; also Morello et al.,1971, Morello & Adámoli, 1974, and Cabrera, 1976.

E- 'Selva de Ribera', Argentina (Prado et al., in press a; Morello & Adámoli, 1974).

F- Gallery Forest, Argentina (Franceschi & Lewis, 1979)

G- Upper Uruguay River Valley Forests, Santa Catarina and Rio Grande do Sul, Brazil (Klein, 1972; Rambo, 1980).

H- Planalto Forest, Vassununga & Bauru, São Paulo, Brazil (Martins, 1979, pp 108-9; Cavassan et al., 1984).

I- Subandean Piedmont Forests, in both its 'Palo blanco' and 'Tipa-Pacará' variants. Floristic list taken from Sect. 4.3.

J- The Caatingas province, Brazil. Floristic list: Sect. 4.2.

K- Calcareous woodlands, Mato Grosso do Sul, Brazil (Ratter et al., 1988b, p.516;Prado et al., in press b).

L- Calcareous forest of Januária, MG, Brazil (Ratter et al., 1978).

M- Dry Caribbean vegetation of Venezuela. The floristic list is an aggregate of Aristeguieta's (1968) "selva veranera" (summer-green forest) and semiarid scrublands (Matteucci & Colma, 1982, pp 102-4).

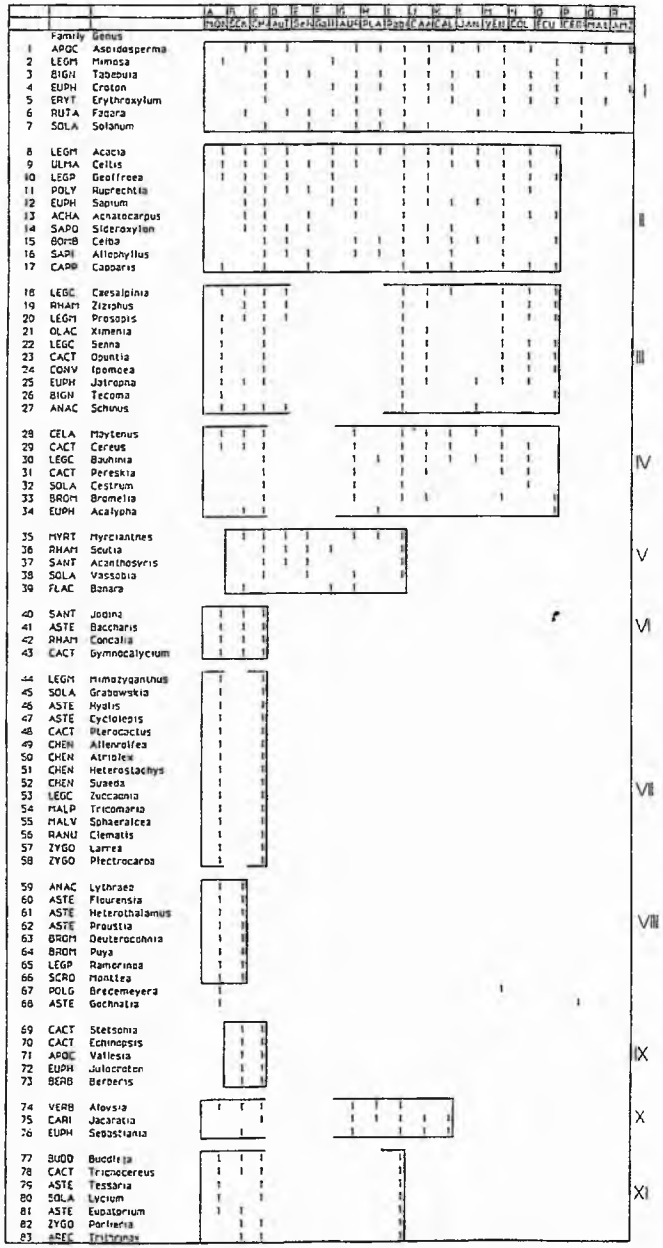
N- Dry Caribbean vegetation of Colombia (Dugand, 1970, pp 428-31; Rieger, 1976, pp 40-1).

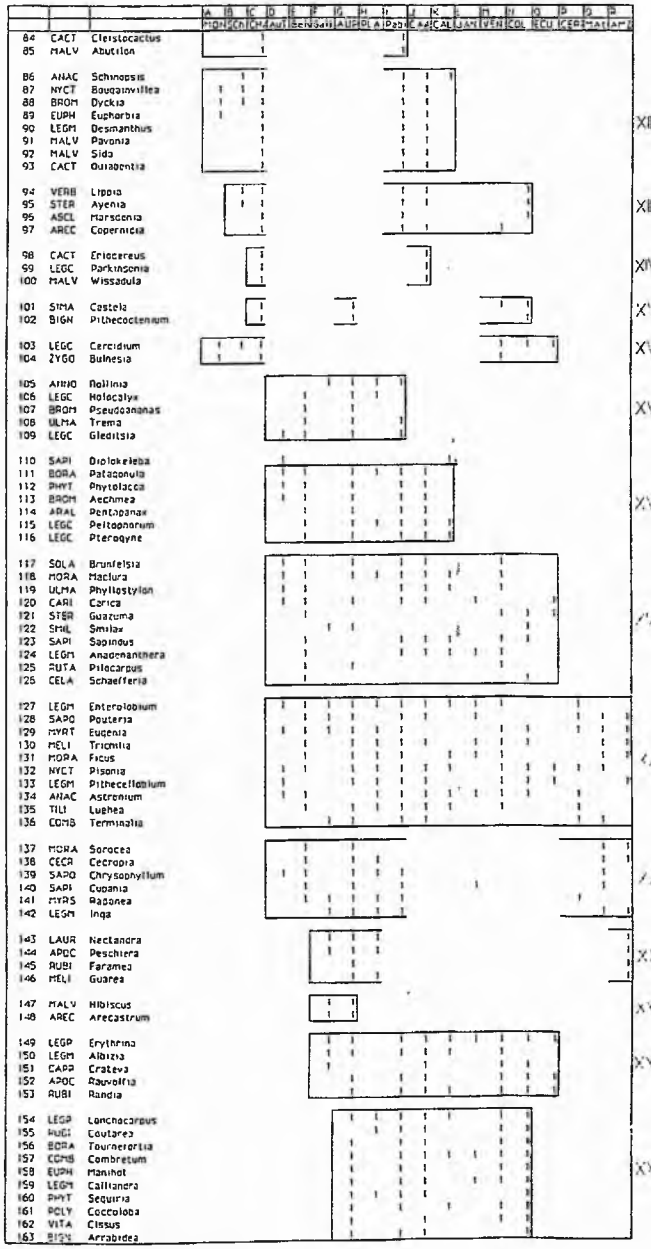
O- Dry forests, woodlands and savannas of W Ecuador, as in Acosta-Solís (1966, pp 413-5) and Harling (1979).

P- Cerrado and cerradão in Brasília, Federal District (Ratter, 1986; P.E. Oliveira, pers. comm.).

Q- Atlantic rainforest , Ubatuba, SP, Brazil (Silva & Leitão Fº, 1982).

R- Amazon forest, km 30 on the road Manaus-Itacoatiara, Amazonas, Brazil (Prance et al., 1976,pp 28-35).


A B C D E F G H I J K L M N O P Q R S
MON ZCA CHA AUT BEN GUI AUP OLA IPO CAA CAL JAN YEN COL ECU CER MAT ANT
1 APOC Aspidosperma
2 LEGM Mimosa
3 BIGN Tabebuia
4 EUPH Croton
5 ERYT Erythroxylum
6 RUTA Fagara
7 SOLA Solanum
8 LEGM Acacia
9 ULMA Celtis
10 LEGP Geoffroea
11 POLY Ruprechtia
12 EUPH Sapium
13 ACHA Achatocarpus
14 SAPO Sideroxylon
15 BOMB Ceiba
16 SAPI Allophyllus
17 CAPP Capparis
18 LEGC Caesalpinia
19 RHAM Ziziphus
20 LEGM Prosopis
21 OLAC Ximenia
22 LEGC Senna
23 CACT Opuntia
24 CONV Ipomoea
25 EUPH Jatropha
26 BIGN Tecoma
27 ANAC Schinus
28 CELA Maytenus
29 CACT Cereus
30 LEGC Bauhinia
31 CACT Pereskia
32 SOLA Cestrum
33 BROM Bromelia
34 EUPH Acalypha
35 MYRT Myrcianthes
36 RHAM Scutia
37 SANT Acanthosyris
38 SOLA Vassobia
39 FLAC Banara
40 SANT Jodina
41 ASTE Baccharis
42 RHAM Condalia
43 CACT Gymnocalycium
44 LEGM Mimozyganthus
45 SOLA Grabowskia
46 ASTE Hyalis
47 ASTE Cyclolepis
48 CACT Pterocactus
49 CHEN Allenrolfea
50 CHEN Atriplex
51 CHEN Heterostachys
52 CHEN Suaeda
53 LEGC Zuccagnia
54 MALP Tricomaria
55 MALV Sphaeralcea
56 RANU Clematis
57 ZYGO Larrea
58 ZYGO Plectrocarpa
59 ANAC Lythraea
60 ASTE Flourensia
61 ASTE Heterothalamus
62 ASTE Proustia
63 BROM Deuterocohnia
64 BROM Puya
65 LEGP Ramorinoa
66 SCRO Monttea
67 POLG Brecemeyera
68 ASTE Gochnatia
69 CACT Stetsonia
70 CACT Echinopsis
71 APOC Vallesia
72 EUPH Julocroton
73 BERB Berberis
74 VERB Aloysia
75 CARI Jacaratia
76 EUPH Sebastiania
77 BUDD Buddleja
78 CACT Trichocereus
79 ASTE Tessaria
80 SOLA Lycium
81 ASTE Eupatorium
82 ZYGO Porlieria
83 AREC Trithrinax
I
II
III
IV
V
VI
VII
VIII
IX
X
XI


A B C D E F G H I J K L M N O P Q R S
MON ZCA CHA AUT BEN GUI AUP OLA IPO CAA CAL JAN YEN COL ECU CER MAT ANT
84 CACT Cleistocactus
85 MALV Abutilon
86 ANAC Schinopsis
87 NYCT Bougainvillea
88 BROM Dyckia
89 EUPH Euphorbia
90 LEGM Desmanthus
91 MALV Pavonia
92 MALV Sida
93 CACT Quiabentia
94 VERB Lippia
95 STER Ayenia
96 ASCL Marsdenia
97 AREC Copernicia
98 CACT Eriocereus
99 LEGC Parkinsonia
100 MALV Wissadula
101 SIMA Castela
102 BIGN Pithecoctenium
103 LEGC Cercidium
104 ZYGO Bulnesia
105 ANNO Rollinia
106 LEGC Holocalyx
107 BROM Pseudoananas
108 ULMA Trema
109 LEGC Gleditsia
110 SAPI Diplokeleba
111 BORA Patagonula
112 PHYT Phytolacca
113 BROM Aechmea
114 ARAL Pentapanax
115 LEGC Peltophorum
116 LEGC Pterogyne
117 SOLA Brunfelsia
118 MORA Maclura
119 ULMA Phyllostylon
120 CARI Carica
121 STER Guazuma
122 SMIL Smilax
123 SAPI Sapindus
124 LEGM Anadenanthera
125 PODA Pilocarpus
126 CELA Schaefferia
127 LEGM Enterolobium
128 SAPO Pouteria
129 MYRT Eugenia
130 MELI Trichilia
131 MORA Ficus
132 NYCT Pisonia
133 LEGM Pithecellobium
134 ANAC Astronium
135 TILI Luehea
136 COMB Terminalia
137 MORA Sorocea
138 CECR Cecropia
139 SAPO Chrysophyllum
140 SAPI Cupania
141 MYRS Rapanea
142 LEGM Inga
143 LAUR Nectandra
144 APOC Peschiera
145 RUBI Faramea
146 MELI Guarea
147 MALV Hibiscus
148 AREC Arecastrum
149 LEGP Erythrina
150 LEGM Albizia
151 CAPP Crateva
152 APOC Rauvolfia
153 RUBI Randia
154 LEGP Lonchocarpus
155 RUGI Coutarea
156 BORA Tournefortia
157 COMB Combretum
158 EUPH Manihot
159 LEGM Calliandra
160 PHYT Sequieria
161 POLY Coccoloba
162 VITA Cissus
163 BIGN Arrabidea
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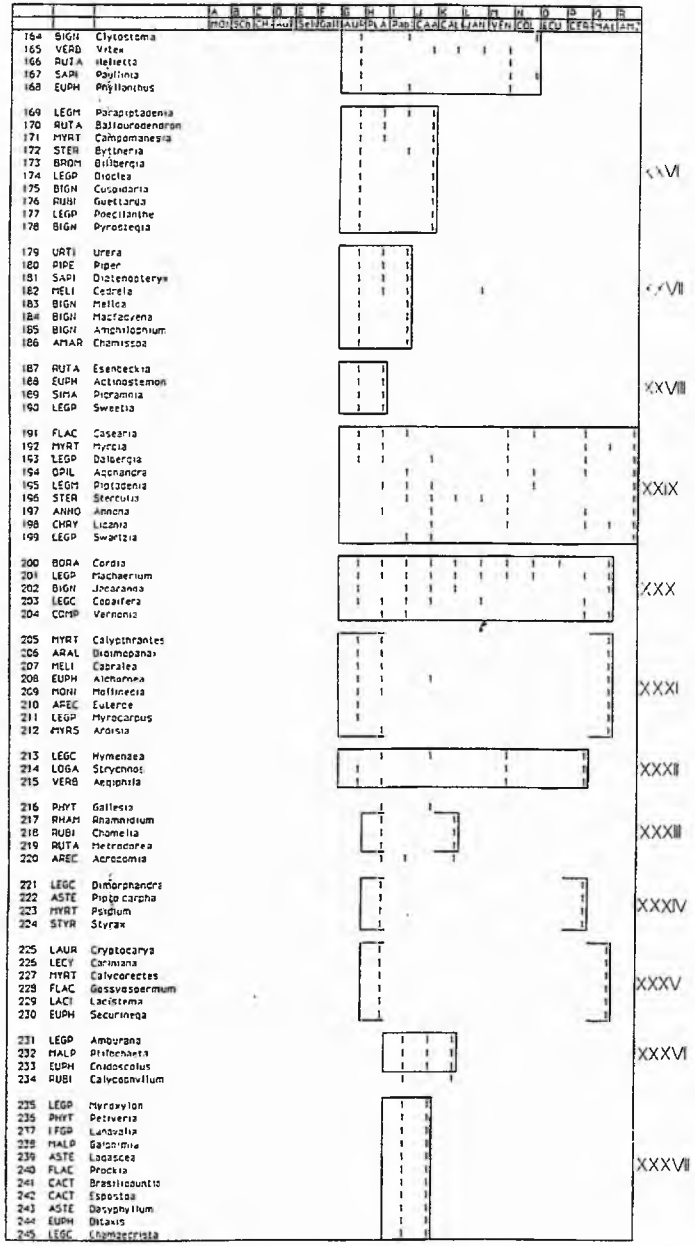
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166 RUTA Helietta
167 SAPI Paullinia
168 EUPH Phyllanthus
169 LEGM Paraptadenia
170 RUTA Balfourodendron
171 MYRT Calyptranthes
172 STER Bytneria
173 BROM Bilbergia
174 LEGP Dioclea
175 BIGN Cuspidaria
176 RUBI Guettarda
177 LEGP Poecilanthe
178 BIGN Pyrostegia
179 URTI Urera
180 PIPE Piper
181 SAPI Dictyoptera
182 MELI Cedrela
183 BIGN Mellca
184 BIGN Macfadyena
185 BIGN Amphilophium
186 AMAR Chamissoa
187 RUTA Esenbeckia
188 EUPH Actinostemon
189 SIMA Picramnia
190 LEGP Sweetia
191 FLAC Casearia
192 MYRT Myrcia
193 LEGP Dalbergia
194 OPIL Agonandra
195 LEGM Piptadenia
196 STER Sterculia
197 ANNO Annona
198 CHRY Licania
199 LEGP Swartzia
200 BORA Cordia
201 LEGP Machaerium
202 BIGN Jacaranda
203 LEGC Copaifera
204 COMB Vernonia
205 MYRT Calyptranthes
206 ARAL Dimorphanax
207 MELI Cabralea
208 EUPH Alchornea
209 MONI Mollinedia
210 AREC Euterpe
211 LEGP Myrocarpus
212 MYRS Ardisia
213 LEGC Hymenaea
214 LOGA Strychnos
215 VERB Aegiphila
216 PHYT Gallesia
217 RHAM Rhamnidium
218 RUBI Chomelia
219 RUTA Metrodorea
220 AREC Acrocomia
221 LEGC Dimorphandra
222 ASTE Piptocarpha
223 MYRT Psidium
224 STYR Styrax
225 LAUR Cryptocarya
226 LECY Carinlana
227 MYRT Calycorectes
228 FLAC Gossypospermum
229 LACI Lacistema
230 EUPH Securinega
231 LEGP Amburana
232 MALP Pfaffchaeta
233 EUPH Cnidoscolus
234 RUBI Calycosmilium
235 LEGP Myroxylon
236 PHYT Petiveria
237 LEGP Lonchocarpus
238 MALP Gaiesiella
239 ASTE Lagascea
240 FLAC Prockia
241 CACT Brasilicactus
242 CACT Espostoa
243 ASTE Dasyphyllum
244 EUPH Ditaxis
245 LEGC Chamaecrista
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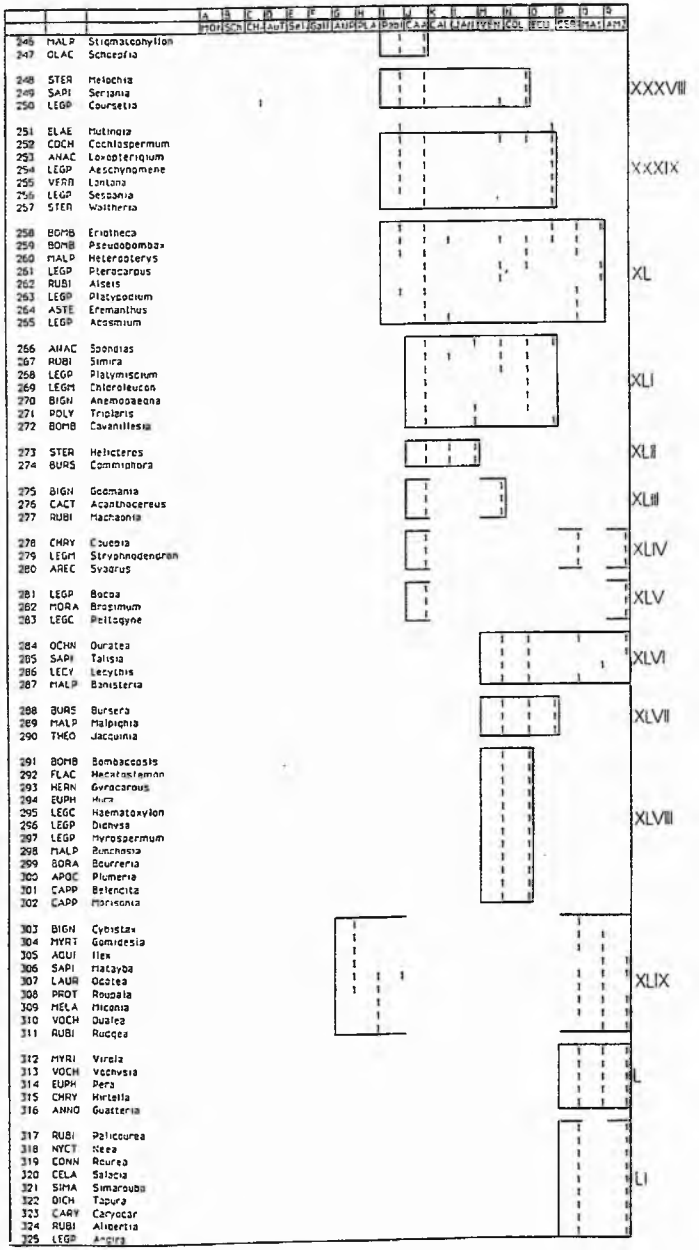
XXXVII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247 OLAC Schoepfia
248 STER Melochia
249 SAPI Serjania
250 LEGP Coursetia
251 ELAE Mutingia
252 COCH Cochlospermum
253 ANAC Loxopterigium
254 LEGP Aeschynomene
255 VERB Lantana
256 LEGP Sesbania
257 STER Waltheria
258 BOMB Eriotheca
259 BOMB Pseudobombax
260 MALP Heteropterys
261 LEGP Pterocarpus
262 RUBI Alseis
263 LEGP Platycyamus
264 ASTE Eremanthus
265 LEGP Acosmium
266 ANAC Spondias
267 RUBI Simira
268 LEGP Platymiscium
269 LEGM Chloroleucon
270 BIGN Anemopaegma
271 POLY Triplaris
272 BOMB Cavanillesia
273 STER Helicteres
274 BURS Commiphora
275 BIGN Geomania
276 CACT Acanthocereus
277 RUBI Machaonia
278 CHRY Couepia
279 LEGM Stryphnodendron
280 AREC Syagrus
281 LEGP Bocoa
282 MORA Brosimum
283 LEGC Peltogyne
284 OCHN Ouratea
285 SAPI Talisia
286 LECY Lecythis
287 MALP Banisteria
288 BURS Bursera
289 MALP Malpighia
290 THEO Jacquinia
291 BOMB Bombacopsis
292 FLAC Hecatostemon
293 HERN Gyrocarpus
294 EUPH Hura
295 LEGC Haematoxylon
296 LEGP Dipteryx
297 LEGP Myrospermum
298 MALP Banisteria
299 BORA Bourreria
300 APOC Plumeria
301 CAPP Belencita
302 CAPP Morisonia
303 BIGN Cybistax
304 MYRT Gomidesia
305 AQUI Ilex
306 SAPI Matayba
307 LAUR Ocotea
308 PROT Roupala
309 MELA Miconia
310 VOCH Qualea
311 RUBI Ruccea
312 MYRI Virola
313 VOCH Vochysia
314 EUPH Pera
315 CHRY Hirtella
316 ANNO Guatteria
317 RUBI Palicourea
318 NYCT Neea
319 CONN Rourea
320 CELA Salacia
321 SIMA Simaruba
322 DICH Tapura
323 CARY Caryocar
324 RUBI Alibertia
325 LEGP Andira
XXXVIII
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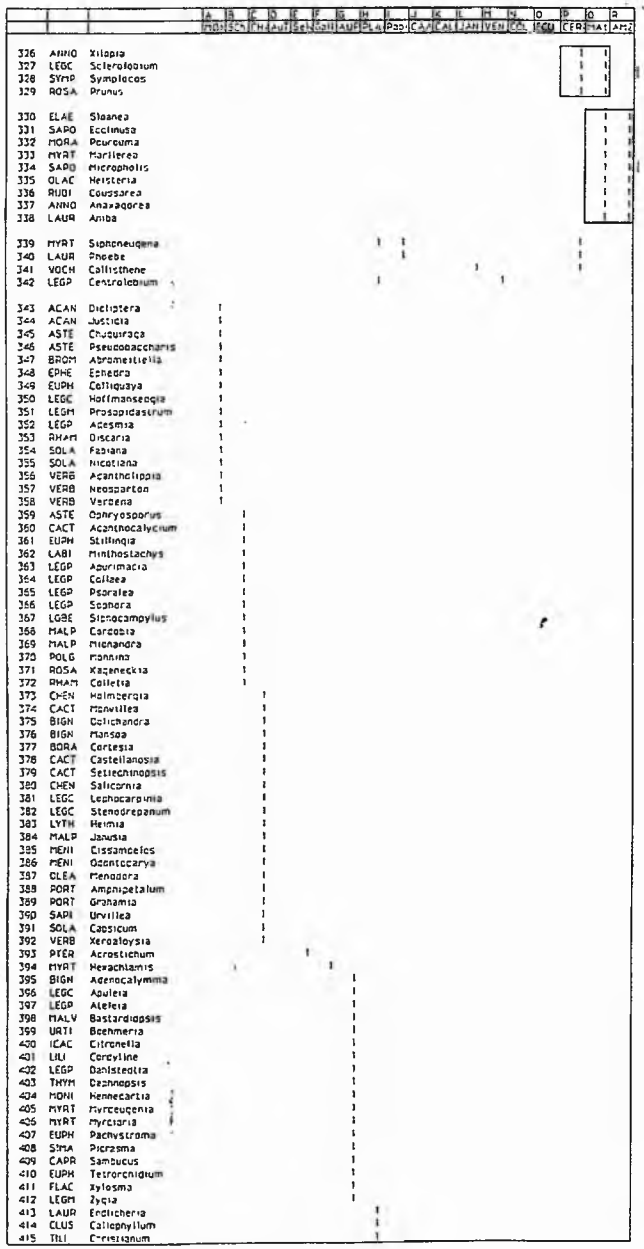
A B C D E F G H I J K L M N O P Q a
MORSCH CHAUTSENGSTLAUPLA PAPCAPCALLJANIVENICOL ICCU CERSMAT APIZ
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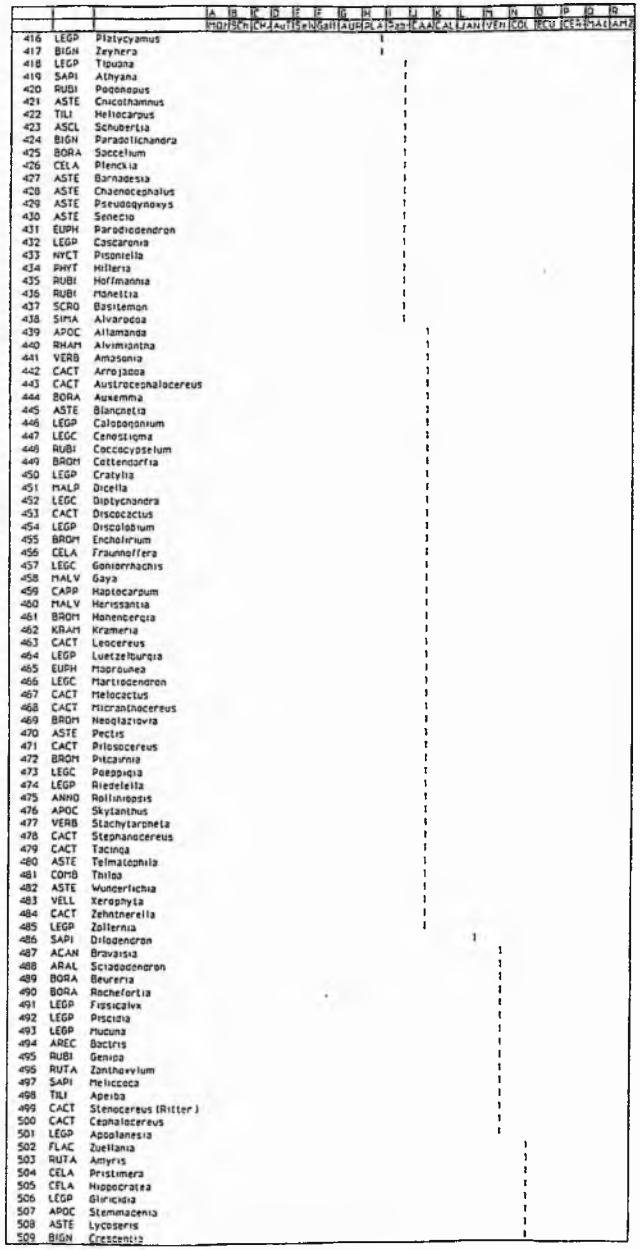
337 LEGC Sclerolobium
338 SYMP Symplocos
339 ROSA Prunus
340 ELAE Sloanea
341 SAPO Ecclinusa
342 MORA Pourouma
343 MYRT Marlierea
344 SAPO Micropholis
345 OLAC Heisteria
346 RUBI Coussarea
347 ANNO Anaxagorea
348 LAUR Aniba
349 MYRT Siphoneugena
350 LAUR Phoebe
351 VOCH Callisthene
352 LEGP Centrolobium
353 ACAN Diclipiera
354 ACAN Justicia
355 ASTE Chaptiraca
356 ASTE Pseudobaccharis
357 BROM Abromeitiella
358 EPHE Ephedra
359 EUPH Colliguaya
360 LEGC Hoffmanseggia
361 LEGM Prosopidastrum
362 LEGP Adesmia
363 RHAM Discaria
364 SOLA Fabiana
365 SOLA Nicotiana
366 VERB Acantholippia
367 VERB Neosparton
368 VERB Verbena
369 ASTE Cnicosporus
370 CACT Acanthocalycium
371 EUPH Stillingia
372 LABI Minthostachys
373 LEGP Apurimacia
374 LEGP Collaea
375 LEGP Psoralea
376 LEGP Sophora
377 LGBE Stenocampylus
378 MALP Cardiopia
379 MALP Menandra
380 POLG Monnina
381 ROSA Kageneckia
382 RHAM Colletia
383 CHEN Helmbergia
384 CACT Manvillea
385 BIGN Dolichandra
386 BIGN Mansoa
387 BORA Cortesia
388 CACT Castellanosia
389 CACT Setiechinopsis
390 CHEN Salicornia
391 LEGC Lophocarpinia
392 LEGC Stenodrepanum
393 LYTH Hemia
394 MALP Janusia
395 MENI Cissampelos
396 MENI Odontocarya
397 OLEA Menodora
398 PORT Amphipetalum
399 PORT Grahamia
400 SAPI Urvillea
401 SOLA Capsicum
402 VERB Xeraloysia
403 PTER Acrostichum
404 MYRT Hexachlamis
405 BIGN Adenocalymma
406 LEGC Apuleia
407 LEGP Aeschynomene
408 MALV Bastardiopsis
409 URTI Boehmeria
410 ICAC Citronella
411 LILI Cordyline
412 LEGP Dahlstedtia
413 THYM Dennisodon
414 MONI Hennecartia
415 MYRT Myrceugenia
416 MYRT Myrcianthes
417 EUPH Pachystroma
418 SIMA Picrasma
419 CAPR Sambucus
420 EUPH Tetrorchidium
421 FLAC Xylosma
422 LEGM Zygia
423 LAUR Endlicheria
424 CLUS Calophyllum
425 TILI Christianum


A B C D E F G H I J K L M N O P Q R
MORSCH CHAUTSENGSTLAUPLA PAPCAPCALLJANIVENICOL ICCU ICES MAEJAMZ
416 LEGP Platycyamus
417 BIGN Zeyhera
418 LEGP Tipuana
419 SAPI Athyana
420 RUBI Pogonopus
421 ASTE Cnicothamnus
422 TILI Heliocarpus
423 ASCL Schubertia
424 BIGN Paradolichandra
425 BORA Saccelium
426 CELA Plenckia
427 ASTE Barnadesia
428 ASTE Chaenocephalus
429 ASTE Pseudogynoxys
430 ASTE Senecio
431 EUPH Parodiodendron
432 LEGP Cascaronia
433 NYCT Pisonielia
434 PHYT Hilleria
435 RUBI Hoffmannia
436 RUBI Manettia
437 SCRO Basistemon
438 SIMA Alvaradoa
439 APOC Allamanda
440 RHAM Alvimiantha
441 VERB Amasonia
442 CACT Arrojadoa
443 CACT Austrocephalocereus
444 BORA Auxemma
445 ASTE Blanchetia
446 LEGP Calopogonium
447 LEGC Cenostigma
448 RUBI Coccocypselum
449 BROM Cottendorfia
450 LEGP Cratylia
451 MALP Dicella
452 LEGC Diptychandra
453 CACT Discocactus
454 LEGP Discolobium
455 BROM Encholirium
456 CELA Fraunhofera
457 LEGC Goniorrhachis
458 MALV Gaya
459 CAPP Haptocarpum
460 MALV Herissantia
461 BROM Hohenbergia
462 KRAM Krameria
463 CACT Leocereus
464 LEGP Luetzelburgia
465 EUPH Maprounea
466 LEGC Martiodendron
467 CACT Melocactus
468 CACT Micranthocereus
469 BROM Neoglaziovia
470 ASTE Pectis
471 CACT Pilosocereus
472 BROM Pitcairnia
473 LEGC Poeppigia
474 LEGP Riedeliella
475 ANNO Rollinieopsis
476 APOC Skytanthus
477 VERB Stachytarpheta
478 CACT Stephanocereus
479 CACT Tacinga
480 ASTE Telmatophila
481 COMB Thilea
482 ASTE Wunderlichia
483 VELL Xerophyta
484 CACT Zehntnerella
485 LEGP Zollernia
486 SAPI Diplodemon
487 ACAN Bravaisia
488 ARAL Sciadodendron
489 BORA Beureria
490 BORA Rochefortia
491 LEGP Fissicalyx
492 LEGP Piscidia
493 LEGP Mucuna
494 AREC Bactris
495 RUBI Genipa
496 RUTA Zanthoxylum
497 SAPI Melicoccus
498 TILI Apeiba
499 CACT Stenocereus (Ritter)
500 CACT Cephalocereus
501 LEGP Appalanesia
502 FLAC Zuelania
503 RUTA Amyris
504 CELA Prestimera
505 CELA Hippocratea
506 LEGP Gliricidia
507 APOC Stemmadenia
508 ASTE Lycoseris
509 BIGN Crescentia

			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
			MON	SCh	CHA	AUT	SeN	GalI	AUR	PLA	Pab	CAA	CAL	JAN	VEN	COL	ECU	CER	MAt	AMZ
510	BIGN	Xylophragma														1				
511	MALP	Hiraea														1				
512	ASCL	Matelea														1				
513	THEO	Clavija															1			
514	CACT	Armatocereus															1			
515	CACT	Hylocereus															1			
516	LEGM	Leucaena															1			
517	ANAC	Anacardium															1			
518	ARAL	Nothopanax															1			
519	ASTE	Wedelia															1			
520	LOGA	Antonia																1		
521	CELA	Austroplenckia																1		
522	MYRT	Blepharocalyx																1		
523	LEGP	Bowdichia																1		
524	AREC	Butia																1		
525	MALP	Byrsonima																1		
526	CELA	Cheiloclinium																1		
527	CONN	Connarus																1		
528	MYRS	Cybianthus																1		
529	DILL	Davilla																1		
530	ARAL	Didymopanax																1		
531	EBEN	Diospyros																1		
532	ICAC	Emmotum																1		
533	RUBI	Ferdinandusa																1		
534	APOC	Hancornia																1		
535	CLUS	Kielmeyera																1		
536	LYTH	Lafoensia																1		
537	MYRT	Pimenta																1		
538	LEGM	Plathymenia																1		
539	LEGP	Pterodon																1		
540	VOCH	Salvertia																1		
541	RUBI	Tocoyena																1		
542	LEGP	Vatairea																1		
543	VELL	Vellozia																1		
544	RUBI	Amaioua																	1	
545	EUPH	Aparisthmium																	1	
546	AREC	Astrocaryum																	1	
547	AREC	Attalea																	1	
548	AREC	Barbosa																	1	
549	RUBI	Bathysa																	1	
550	CLET	Clethra																	1	
551	PROT	Euplassa																	1	
552	MELA	Henriettella																	1	
553	EUPH	Hyeronima																	1	
554	LEGP	Hymenolobium																	1	
555	CUNO	Lamanonia																	1	
556	EUPH	Mabea																	1	
557	LEGM	Macrosamanea																	1	
558	APOC	Malouetia																	1	
559	LEGM	Pseudopiptadenia																	1	
560	RUBI	Psyc																	1	
561	CLUS	Rheedia																	1	
562	ASTE	Stifftia																	1	
563	ANAC	Tapirira																	1	
564	APOC	Ambelania																		1
565	VIOL	Amphirrox																		1
566	APOC	Anacampta																		1
567	ANNO	Bocageopsis																		1
568	BOMB	Bombacopsis																		1
569	COMB	Buchenavia																		1
570	MYRT	Calyptranthes																		1
571	RUBI	Chimarrhis																		1
572	EUPH	Conceveiba																		1
573	LECY	Corythophora																		1
574	LECY	Couratari																		1
575	LEGP	Dipteryx																		1
576	DUCK	Duckeodendron																		1
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580	LEGC	Eperua																		1
581	ANNO	Ephedranthus																		1
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583	VOCH	Erisma																		1
584	LECY	Eschweilera																		1
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586	APOC	Geissospermum																		1
587	GNET	Gnetum																		1
588	MORA	Helianthostylis																		1
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590	LECY	Holopyxidium																		1
591	MYRI	Iryanthera																		1
592	FLAC	Laetia																		1
593	VIOL	Leonia																		1
594	LAUR	Licaria																		1
595	OLAC	Limasma																		1
596	TILI	Lueheopsis																		1
597	LEGC	Macrolobium																		1
598	MORA	Maquira																		1
599	OLAC	Minquartia																		1
600	MELA	Mourirla																		1
601	MORA	Naucleopsis																		1
602	SAPO	Neoxythece																		1
603	AREC	Oenocarpus																		1

			1A	1B	1C	1D	1E	1F	1G	1H	1I	1J	1K	1L	1M	1N	1O	1P	1Q	1R
			MON	SCh	CHA	AuT	ISe	NGa	IIA	UR	BLA	Pab	IIC	AA	ICA	LJA	NIV	EN	ICO	L.	ECU	ICE	RÁM	AS	AM	Z
604	CHRY	Parinari																								1
605	VIOL	Paypayrola																								1
606	EUPH	Pogonophora																								1
607	SAPO	Prieurella																								1
608	SAPO	Pseudolabatia																								1
609	QUIIN	Quiina																								1
610	SAPO	Richardella																								1
611	VIOL	Rinorea																								1
612	HUMI	Saccoglottis																								1
613	BOMB	Scleronema																								1
614	MONI	Siparuna																								1
615	BURS	Tetragastris																								1
616	STER	Theobroma																								1
617	CLUS	Tovomita																								1
618	MORA	Trimatococcus																								1
619	ANNO	Unonopsis																								1

7. THE ZOOLOGICAL EVIDENCE

7.1- The avian evidence:

The strongest evidence which apparently supports the alleged biogeographical link between the Chaco and the Caatingas has come from the zoological field. In a landmark paper, Short (1975) analyzed the Chaco avifauna, and based on what he regarded as a "markedly low endemism" and "the very close affinities with surrounding avifaunas" concluded that "the 'chaco avifauna' [*is*] a nonentity, the term being useful only in a strictly distributional context" (Short, *op . cit* ., p.329). All other biogeographical areas of South America – divided in two groups: regions adjacent to and regions distant from the Chaco – were compared to his bird species list. Five out of the six neighbouring regions showed very high numbers of common species with the Chaco (e.g. 311 bird taxa in common with the Cerrados), whereas amongst the distant regions the Caatingas proved to have the strongest link: 248 species. The elevated figures of common species between the Chaco and the distant Caatingas attracted the attention of biogeographers (Cabrera & Willink, 1980; Bucher, 1982a; Haffer, 1985) and has seemed to give solid support to the Chaco-Caatingas link. However, an attempt will be made here to analyze in closer detail the component distribution of the bird species discussed by Short (1975).

At the outset, it is important to note that Short's concept of the Chaco differs from that employed by various authorities, and also that used in the present study (as discussed in Ch. 2 & 8). Short (1975, Fig.1) shows an area latitudinally wider and meridianally shorter than that of the actual Chaco according to most authors. He included within it not only the whole of the Eastern Chaco (whose phytogeographical identity is under discussion here), but also a good deal of Paraguay east of the Chaco region which can hardly be considered as part of it. The western sector of the Pantanal is apparently also shown as Chaco in Short's map, an area with little real contact with true Chaco vegetation (Prado et al., in press, b). To the south of the region, Short omitted a considerable area which is the southwestern tip of the Chaco, comprising NW Córdoba, E La Rioja and N San Luis (compare with Ragonese & Castiglioni's [1970] map of the Argentine Chaco). Thus, a lot of tropical and subtropical wetter areas in the north and east of the region were added to the core

area of the Chaco, together with their avifaunas, while the temperate and very dry sectors in the south and very particularly the southwest were excluded by Short.

As a result of these peculiar geographical limits set by Short (1975) the Chaco avifauna was bound to be a 'nonentity'. A good deal of tropical birds of more humid areas elsewhere in South America were encompassed within the 409 list of species for the Chaco provided by Short, which was in sharp contrast with the 220 species listed by Olrog (1963a) for the Argentine Chaco. This latter figure seems much more realistic, given the low environmental diversity in the region, even allowing for an increase in the number of species when the Bolivian and Paraguayan Chaco are included to make it comparable to Short's study. Thus, a number of elements alien to the Chaco *s.s.* were included in the list, which in fact only occur marginally in definitely non-chaquenian areas such as the Pantanal (Mato Grosso do Sul), E Paraguay or along the major river systems bordering the Chaco such as the Paraguay and Paraná watercourses. The addition of such species diminished the relevance of the authentic chaquenian elements, a fact already noted by Müller (1973, p.143), while conversely this increase of elements coming from more humid areas did not incorporate any new endemics to the Chaco *sensu* Short. In Short's view, there is only one endemic species (*Eudromia formosa*), and three endemic subspecies in the Chaco. However, if the missing SW chaquenian sector is added, the region recovers its biogeographical homogeneity since it is a well-defined natural area with concrete and characteristic environmental features (see Ch. 2), and several Chaco bird species can be once again regarded as endemisms.

In Table 7.1 the endemic birds of the Chaco are listed; the source of this information comes mainly from Short (1975), both his maps and comments on the range of distribution, cross-checked with Cory & Hellmayr (1924), Olrog (1963a & b), Vaurie (1964 & 1980), Meyer de Schauensee (1966), Short (1971 & 1976), Müller (1973), and Haffer (1985). On this basis, the Chaco biogeographical region comprises one endemic monotypic genus (*Chunga*), seven endemic species and at least four endemic subspecies in its avian fauna, so that it can be considered a well-defined faunal dispersal centre (*sensu* Müller, 1973). It should be

TABLE 7.1:**Birds endemic to the Chaco.**

	Taxon endemic
RHEIDAE	
Rhea americana araneipes	subsp
TINAMIDAE	
Nothura maculosa chacoensis	subsp
Nothura maculosa pallida	subsp
Nothura maculosa paludivaga	subsp
Eudromia formosa	sp
CRACIDAE	
Ortallis canicollis	sp
CARIAMIDAE	
Chunga burmeisteri	genus
PICIDAE	
Dryocopus schulzi	sp
FURNARIIDAE	
Furnarius cristatus	sp
TYRANNIDAE	
Pseudocolopteryx dillenianus	sp
EMBERIZIDAE	
Lophospingus pusillus	sp

pointed out that this list (Table 7.1) and the subsequent one (Table 7.2), do not pretend to be exhaustive at the **subspecific** level but simply aim to record the most outstanding forms of otherwise widespread species.

The Caatingas are richer in avian endemisms as Table 7.2 shows, which must be essentially due to their far greater environmental diversity in comparison with the Chaco plains (cf. Ch. 2 & 4). This table is derived from careful study of the information provided principally in Hellmayr (1929) and Meyer de Schauensee (1966), but also Cory & Hellmayr (1924), Naumburg (1939), Müller (1973), Coelho (1978), Vaurie (1980), Haffer (1985), Leite (1987) and Silva (1989). There are three monotypic genera endemic to the Caatingas (*Cyanopsitta*, *Megaxenops* and *Rhopornis*), and ten endemic species and at least ten subspecies. The number of endemic genera could be doubled if those presently submerged in synonymy *Nyctipolus* (=*Caprimulgus*), *Anopetia* (=*Phaethornis*) and *Gyalophylax* (=*Synallaxis*) genera were accepted as distinct.

There are considerable differences, not only quantitative but also qualitative, between the endemic taxa to the Chaco and to the Caatingas. The Chaco is richer in elements of southerly origin, such as the very important family Tinamidae. For instance, the genus *Nothura* reaches its highest diversity in the region, and this is essentially a Patagonian-Andean-Pampean-Chaquenian genus barely extending into the Caatingas (Short, 1975), while the genus *Eudromia* does not even reach the Pantanal. In contrast, the genus *Crypturellus* in the same family is basically tropical-Amazonian, with several species in the Caatingas and only one species widespread throughout the Chaco (*C. tataupa tataupa*) where the genus finds its southernmost expansion. In the Caatingas the families with an outstanding degree of endemicity are the Psittacidae, Furnariidae and very specially the Formicariidae, which contrarywise, show scarce or no endemism in the Chaco.

It should also be emphasized that between the endemics of both areas there are no cases of very close relatives, with one endemic in either formation and none elsewhere, and likewise no pairs of congeneric, endemic species which would indicate a very strong link. An apparent exception, the case of the caatinga endemic subspecies of

TABLE 7.2: **Birds endemic to the Caatingas.**

	Taxon endemic
TINAMIDAE	
Crypturellus noctivagus zabele	subsp
Nothura maculosa cearensis	subsp
CRACIDAE	
Penelope jacucaca	sp
COLUMBIDAE	
Columba picazuro marginalis	subsp
PSITTACIDAE	
Anodorhynchus leari	sp
Aratinga cactorum cactorum	subsp
Cyanopsitta spixii	genus
CAPRIMULGIDAE	
Caprimulgus (=Nyctipolus) hirundinaceus	sp (genus)
TROCHILIDAE	
Phaethornis (=Anopetia) gounellei	sp (genus)
PICIDAE	
Picummus limae	sp
DENDROCOLAPTIDAE	
Lepidocolaptes squamatus wagleri	subsp
Xiphocolaptes falcirostris	sp
FURNARIIDAE	
Megaxenops parnaguae	genus
Synallaxis (=Gyalophylax) hellmayri	sp (genus)
FORMICARIIDAE	
Formicivora iheringi	sp
Rhopornis ardesiaca	genus
Sakesphorus cristatus	sp
Thamnophilus caerulescens cearensis	subsp
CONOPOPHAGIDAE	
Conopophaga lineata cearae	subsp
TYRANNIDAE	
Idioptilon mirandae mirandae	subsp
Phyllomyias fasciatus cearae	subsp
Phylloscartes roquettei	sp
TROGLODYTIDAE	
Thryothorus longirostris bahiae	subsp

Nothura maculosa , is in fact negligible since this species is widespread in southern South America (see Short, 1975, Fig. 16). Short (1975, Fig. 15) indicates the contrary when he mapped the ranges of distribution of both *Nothura boraquira* and *Myrmorchilus strigilatus* with two disjunct nuclei in the Caatingas and northern Chaco. However, the ranges of these species need to be analyzed in detail, as below.

7.2- Avian patterns of distribution:

In his study Short (1975, p. 337) listed 16 species as disjuncts between the Chaco and the Caatingas (Table 7.3). None of them occur exclusively in the Chaco and the Caatingas and nowhere else; on the contrary, all of them can be found in at least one other biogeographical natural zone (generally neighbouring areas to either of them), and some do not occur in the Chaco *s.s.* at all. The first listed species is *Nothura boraquira* (Tinamidae). In Fig. 7.1 all known localities for this species are shown (Conover, 1950; Short, 1975 & 1976). It is evidently a true caatinga bird, extending even to a locality in Maranhão very close (a few kilometers away) to those indicated by Bigarella et al. (1975) as disjunctions of the Caatingas vegetation in that state. This Tinamidae then reappears in Santa Cruz de la Sierra and Chiquitos areas in Bolivia, close to but out of bounds of the Chaco, and finally there is a group of collections in the more humid Eastern Chaco in Paraguay. Closely following the distribution of *Nothura boraquira* is the Furnariidae *Pseudoseisura cristata* (Fig. 7.2), with the nominate[1] subspecies in the Caatingas, and *P. cristata unirufa* spreading along the upper Paraguay river in SW Brazil and Paraguay, and across E Bolivia to Santa Cruz and El Beni.

A very similar pattern of distribution is followed by *Myrmorchilus strigilatus* (Fig. 7.3), again a true caatinga species with disjunctions in the area usually regarded as Eastern Chaco on the western bank of the river Paraguay, from Urucum (a calcareous hill close to Corumbá in Mato Grosso do Sul) to the river Bermejo in the Formosa province, Argentina. To the west of the Chaco this Formicariidae is restricted to the Subandean Piedmont Forests from Santa Cruz in Bolivia to eastern Jujuy in Argentina (Cory & Hellmayr,

[1] The term "nominate" in Zoology equates to "typical" as employed in plant systematics.

TABLE 7.3: **Alleged Chaco–Caatingas disjuncts (Short, 1975).**

TINAMIDAE
Nothura boraquira
RALLIDAE
Aramides ypecaha
Porzana albicollis
COLUMBIDAE
Columba picazuro
PSITTACIDAE
Aratinga acuticauda
CUCULIDAE
Coccyzus cinereus
STRIGIDAE
Glaucidium minutissimum
FURNARIIDAE
Synallaxis (=Schoeniophylax) phryganophila
Pseudoseisura cristata
FORMICARIIDAE
Myrmorchilus strigilatus
COTINGIDAE
Xenopsaris albinucha
TYRANNIDAE
Xolmis irupero
Stigmatura budytoides
ICTERIDAE
Molothrus badius
Icterus icterus

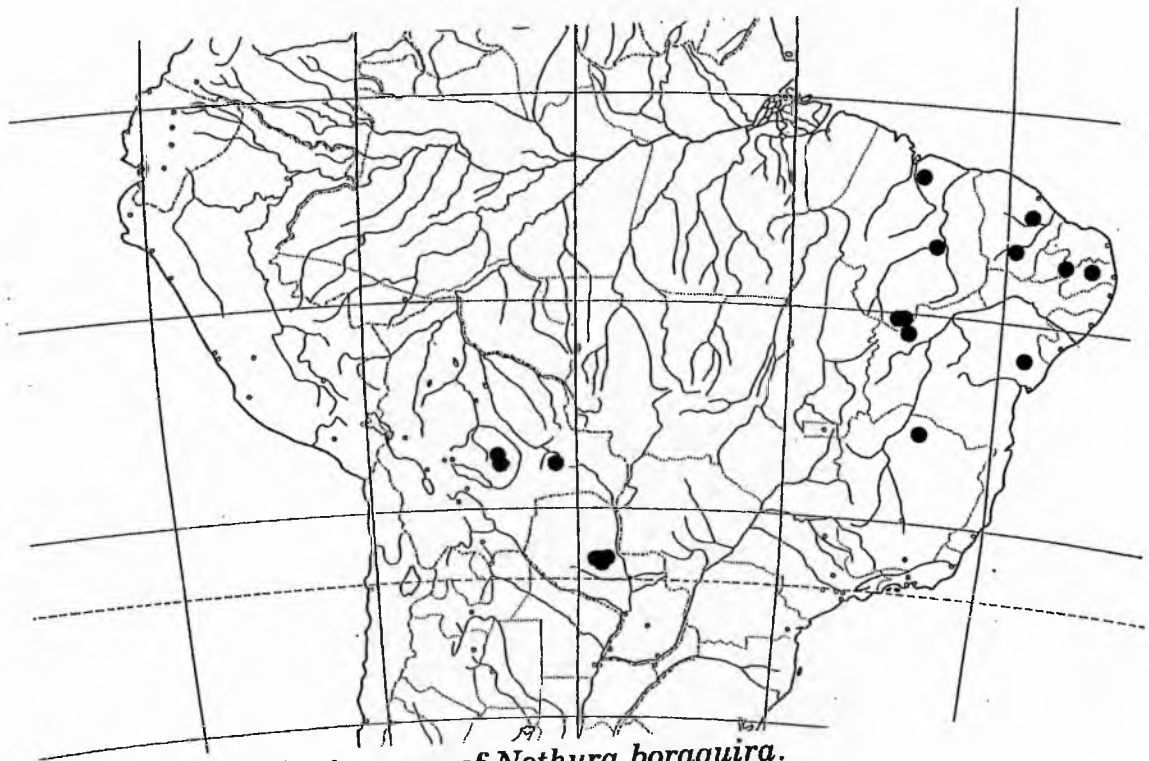
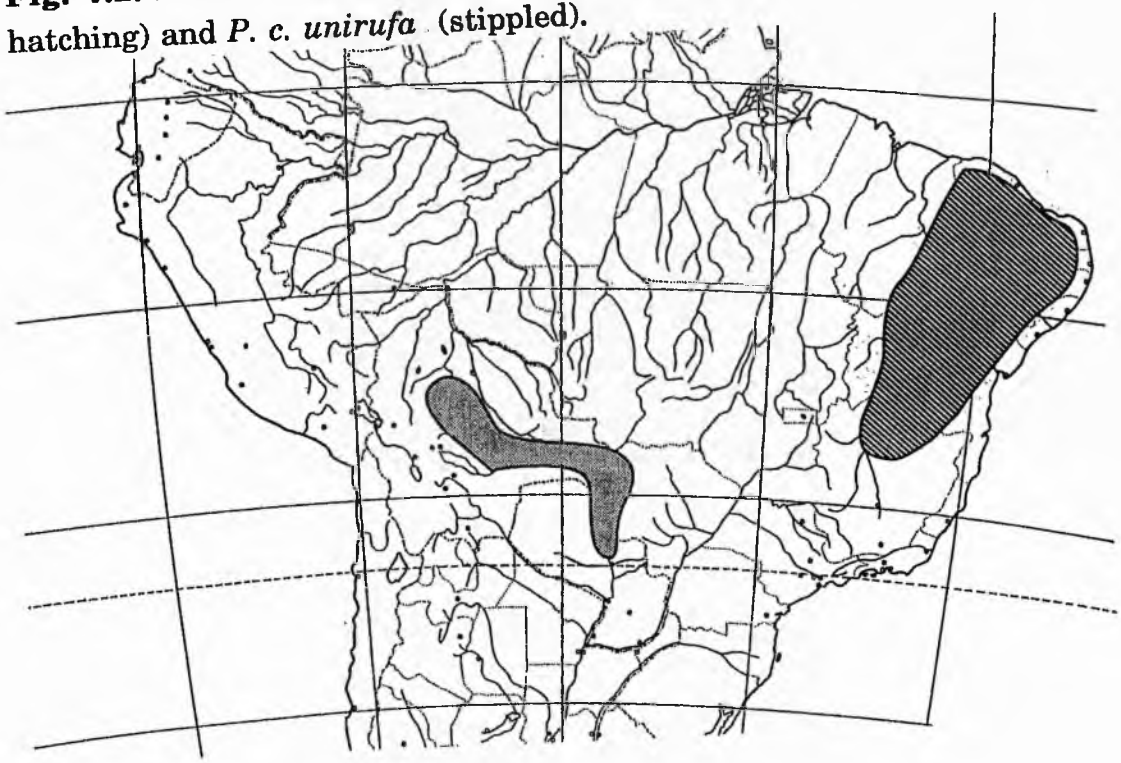


Fig. 7.1: Distribution map of *Nothura boraquira*.

Fig. 7.2: Distribution map of *Pseudoseisura cristata cristata* (oblique hatching) and *P. c. unirufa* (stippled).



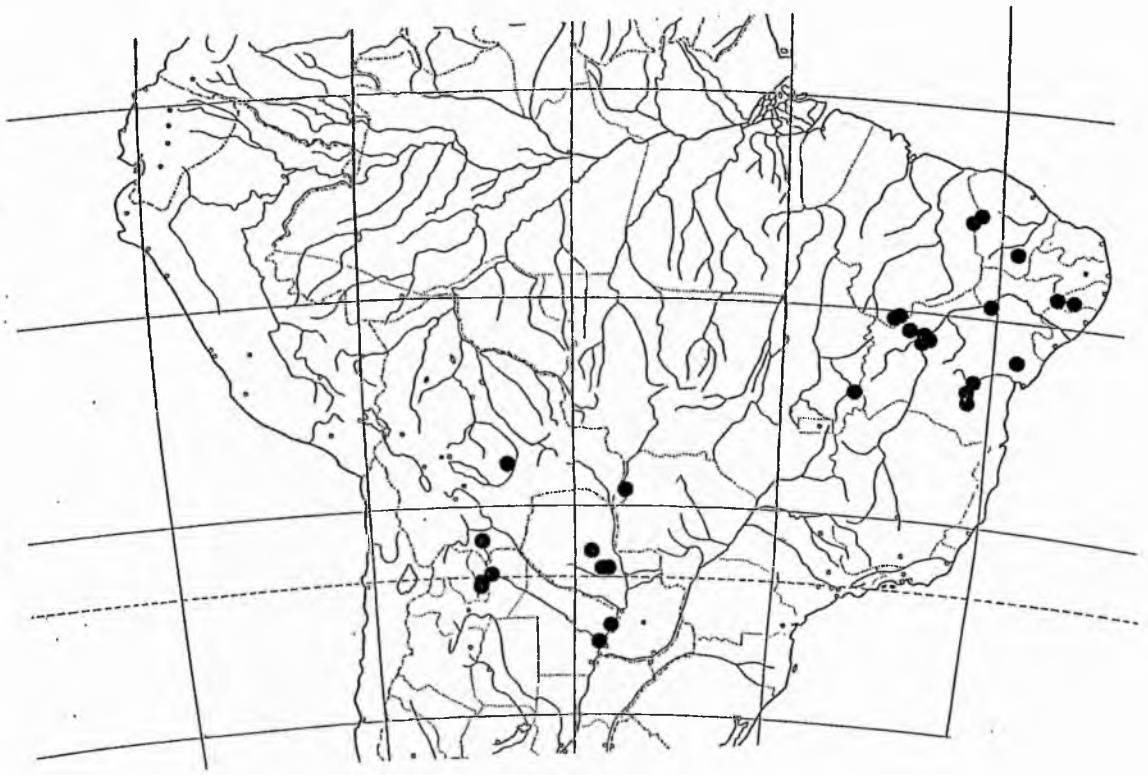


Fig. 7.3: Distribution map of *Myrmorchilus strigilatus* .

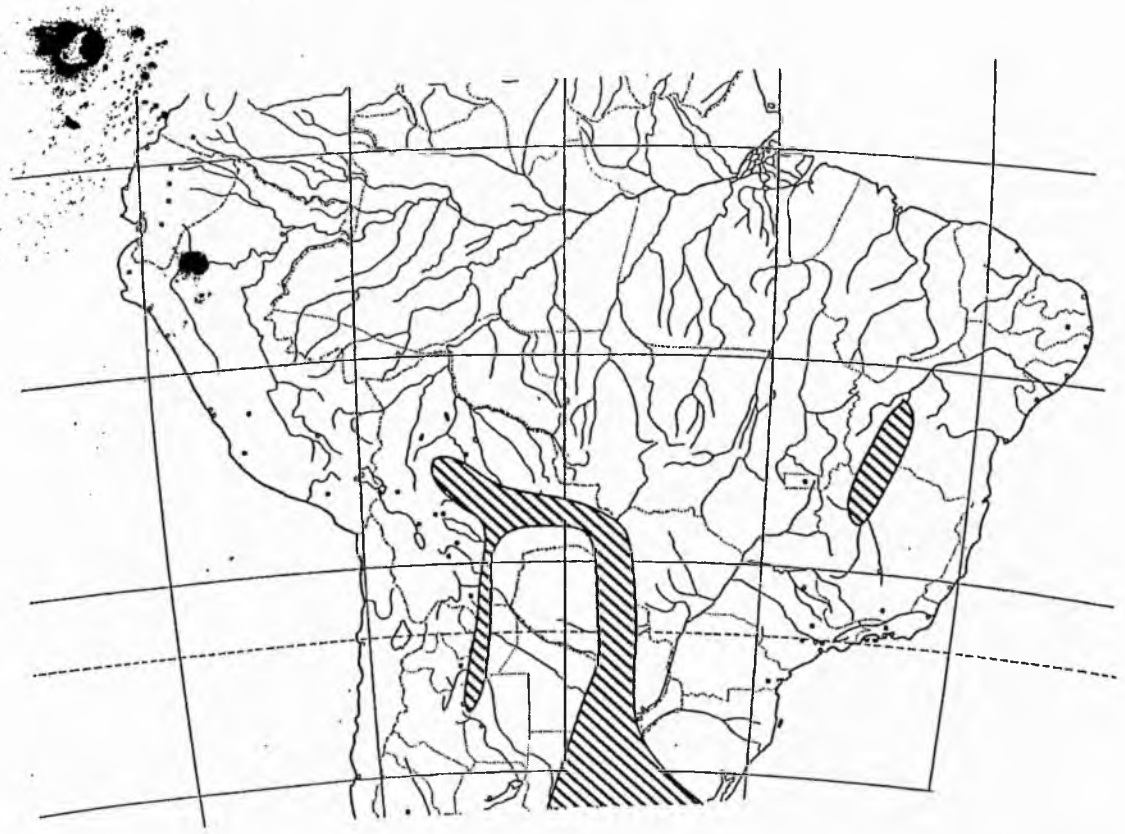


Fig. 7.4: Distribution map of *Synallaxis* [*Schoeniophylax*]*phryganophila*.

1924; Naumburg, 1939). Thus both *Nothura boraquira* and *Myrmorchilus strigilatus* leave in fact a huge blank in their range of distribution in between two N-S orientated arms. This blank corresponds to the main bulk of the Chaco *s.s.* , contrary to Short's map in his Fig. 15.

Another such a case is the Furnariidae *Synallaxis phryganophila* (Fig. 7.4), previously considered a monotypic genus, *Schoeniophylax* , but later submerged into *Synallaxis* by Vaurie (1980), though still as the only monotypic subgenus. The present author has been unable to trace itemized lists of localities for this species, but its distribution can be reconstructed from Olrog (1963a), Meyer de Schauensee (1966), Short (1975) and Vaurie (1980). This bird shows again a blank for the area occupied by the Chaco, surrounding it from west, north and east, and with an additional expansion of range to the Argentine Mesopotamia, Rio Grande do Sul in Brazil, and Uruguay. On the other hand, it occupies a reduced sector in the middle São Francisco river within the Caatingas. It is reported in the literature (Vaurie, 1980) that it can reach the Santiago del Estero province in Argentina, but owing to the nature of its general pattern of distribution (highly coincidental with the Pleistocenic Arc, see Sect. 5.3.1) it is likely to appear there only in upland areas such as those in the west of the province or some isolated low-altitude hills in the extreme northwest, e.g. Cerro del Remate.

There is another group of species, amongst those listed by Short (1975) as Chaco-Caatingas disjuncts, which are certainly Chaco avian elements, and which do also occur in the Caatingas. However, they are not restricted to the Chaco area itself but spread widely on to neighbouring and distant formations. This is the case of the Tyranniidae *Xolmis irupero* (Fig. 7.5), with a geographical race *nivea* in the central dry area of the Caatingas (Short, 1975; Fitzpatrick, 1980), whilst the nominate form occurs in the Beni department in Bolivia (Cabot et al., 1986) south to SE Bolivia, SW Mato Grosso do Sul in Brazil, practically all of Paraguay, the dry subtropical forests in the Subandean piedmont, the Chaco-Pampean plains and Mesopotamia in Argentina, the Uruguay Republic and adjoining Rio Grande do Sul in SE Brazil, extending west into San Juan and Mendoza at the foothills of the Andes.

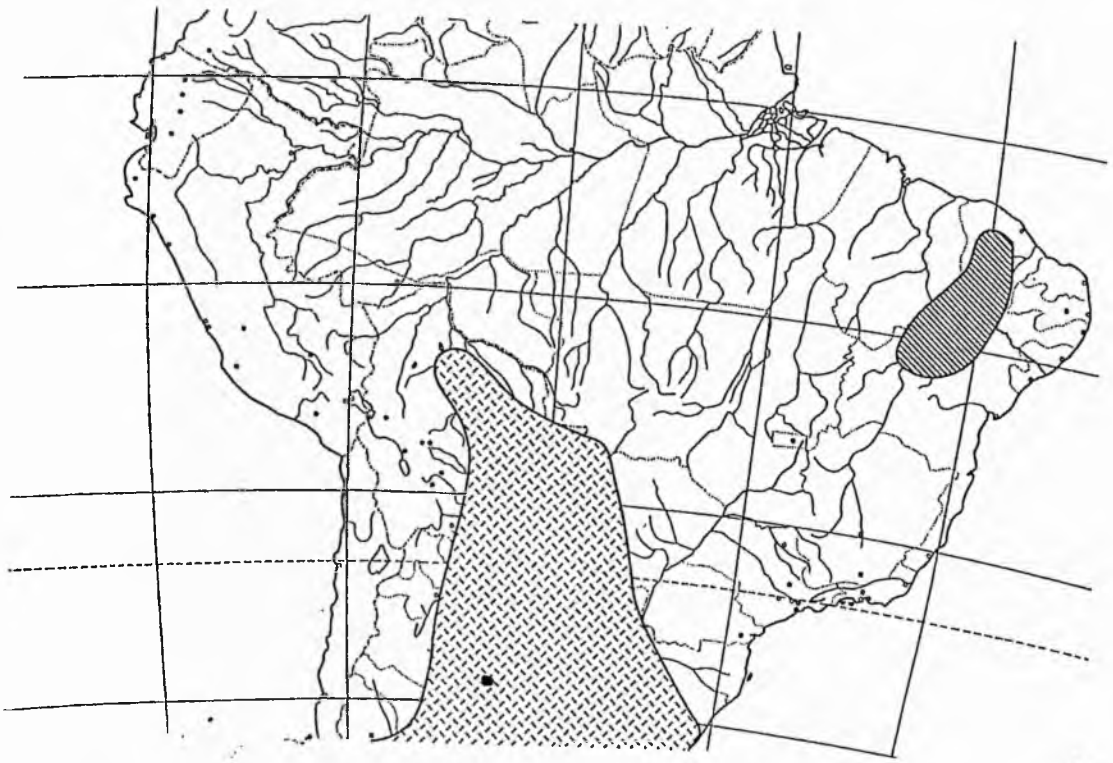


Fig. 7.5: Distribution map of *Xolmis irupero irupero* (race *nivea* in oblique hatching).

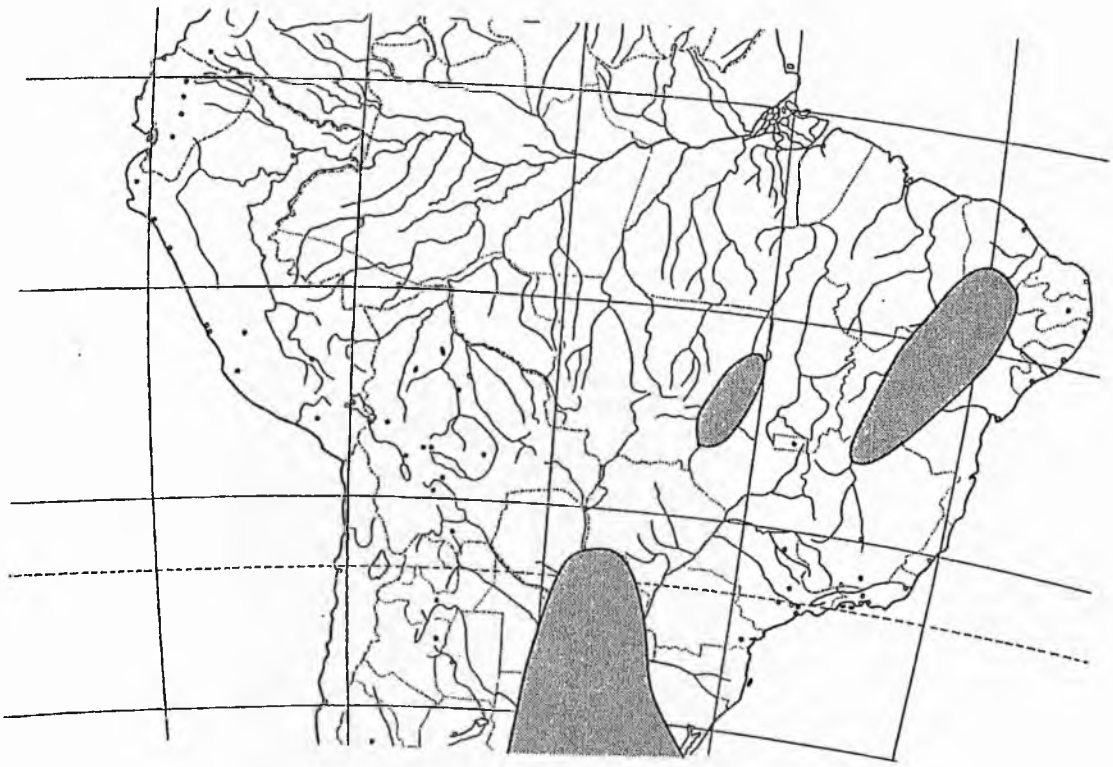


Fig. 7.6: Distribution map of *Aramides ypecaha*.

The disjunction in this species is obviously much wider than simply a Chaco-Caatingas one, but it includes the Moxos savannas in NE Bolivia, subtropical rainforests in E Paraguay, Misiones and Rio Grande do Sul, the treeless Pampas and the semidesert of the Monte in W Argentina.

Other cases reported by Short as Chaco-Caatingas disjuncts but which in fact are similarly more widespread are: *Columba picazuro* (Columbidae), isolated in Caatingas and spreading throughout the Subandean piedmont, Chaco and Pampas, the Paraguay-Paraná river system, and occasionally reaching N Patagonia (Olrog, 1963a); *Aratinga acuticauda* (Psittacidae), occurring in N Colombia and Venezuela, disjunct in the Caatingas, and then reappearing in the Subandean piedmont, Chaco, Argentine Mesopotamia, Pampas and Espinal; the Tyranniidae *Stigmatura budytoides* occurs in the Caatingas in isolation(Short, 1975; Fitzpatrick, 1980), but then is distributed mainly in W Argentina from the Rio Negro province in Patagonia, throughout the Monte and the Subandean piedmont in Argentina and Bolivia (Tarija, Santa Cruz de la Sierra), and apparently also extends into dry Andean valleys in Cochabamba and Chuquisaca, and barely reaches the Chaco in its SW sector; *Molothrus badius* (Icteridae) is the most widespread species of this set of cases, with isolated populations in the Caatingas but with a continuous distribution from central Bolivia and Mato Grosso in the Pantanal, throughout Paraguay, the Paraguay-Paraná river system, the dry forests in the Subandean piedmont (Vuilleumier, 1986), Chaco, Pampas and Monte to Rio Grande do Sul and Uruguay, being sometimes accidental in Chile across the Andes.

A different case is posed by the cuckoo *Coccyzus cinereus* (Cuculidae) which should be considered as a Chaco-dry Caribbean area disjunct as shown in Short's map of Fig. 29, while its presence in the Caatingas remains unproven. This cuckoo has been reported as an accidental migrant in the São Francisco river in Bahia and also in Goiás (Meyer de Schauensee, 1966), but it is not listed for the Caatingas or Goiás by Hellmayr (1929), Coelho (1978), Leite (1987) or Silva (1989). It is a widespread species not only in the Chaco but also in NW Bolivia (Cabot et al., 1986), E Paraguay, Argentine Mesopotamia, the Pampas and to the west into the Monte and the Subandean piedmont (Short, 1975). Also different is the range of distribution of the Aramidae *Aramides ypecaha*

(Fig. 7.6), disjunct in NE Brazil (Bahia, Piauí, etc.), E Mato Grosso, and then from E Paraguay and Misiones south to Buenos Aires following the major water-systems (Paraguay, Paraná and Uruguay rivers), and east to Rio Grande do Sul and Uruguay. Within the Chaco this wood-rail is confined to the Eastern Chaco, whose phytogeographical position will be discussed later.

The remaining five species of the 16 alleged disjuncts listed by Short (1975) share a common factor:they are completely or nearly completely absent from the Chaco *s.s.* . The Rallidae *Porzana albicollis* shows a very exciting range (Fig. 7.7), following the Tropical and Subtropical Seasonal Forests Pattern described in Sect. 5.3.2.. It occurs in the dry Caribbean coast of Colombia and Venezuela, dry interandean valleys in SW Colombia, some parts of the Orinoco river valley and in the Guianas. The collections from around Obidos and Santarem in the Amazon valley are noteworthy, since this is an area where some caatinga tree species have been collected as well. There seems to be a continuous distribution from central Caatingas to Minas Gerais and São Paulo, to then reappear in the Paraguay-Paraná river system involving much of E Paraguay, Misiones and NW Corrientes. Finally, whilst being absent from the Chaco, it is reported for the deciduous forests in NW Argentina and central Bolivia from Santa Cruz de la Sierra to La Paz.

To some extent the Strigidae *Glaucidium minutissimum* overlaps the previous pattern of distribution, spreading from Mexico and Panamá to NW Colombia, with an Amazonian nucleus in Guyana and adjoining Roraima, Amapá and Pará in Brazil, occurring in the Caatingas of Bahia and with disjunct populations in Mato Grosso and NE Paraguay, but not recorded for the Chaco. The Cotingidae *Xenopsaris albinucha minor* (Fig. 7.8) occurs in two apparently isolated areas in Venezuela, whereas the nominate form is known from the Caatingas, and also disjunct populations along the Paraguay-Paraná river valleys, in the Córdoba hills and the Subandean Piedmont Forests in NW Argentina, and in El Beni in Bolivia. This distribution clearly contradicts Short's map (1975, Fig. 45) in which he showed *X. albinucha albinucha* covering the whole of the Chaco. The map of Fig. 7.8 follows Olrog (1963a, p. 23) who cites this cotingidae for both subtropical areas on

Fig. 7.7: Distribution map of *Porzana albicollis*.

Fig. 7.8: Distribution map of *Xenopsaris albinucha* race *albinucha* (race *minor* : more heavily lined area).

the east and west of the Chaco, but not for the Chaco itself (Olrog, 1963a, p. 28-29). Finally, the Icteridae *Icterus icterus* (Fig. 7.9) has a distribution similar to that of *Porzana albicollis* (see Fig. 7.7), but it is much more widespread in the central Amazon, the Caatingas and part of the Cerrados, and it occurs in SW Ecuador and NW Peru, from where *P. albicollis* is absent. *Icterus icterus* is not entirely absent from the Chaco since Short (1976) found collections from the Eastern Chaco in Lichtenau, Paraguay.

A number of other bird species which are listed in the 409 'Chaco' species by Short (1975) do not occur within the Chaco *s.s.* or only marginally in certain parts of Eastern Chaco. Some of these birds in fact follow a distribution range which resembles that of some of the typical caatinga tree species. One such example is the range of *Herpsilochmus pileatus* (Fig. 7.10), of which the typical form is essentially a Caatinga element (Hellmayr, 1929) with a disjunct collection in the area of Chiquitos, Bolivia (Olrog, 1963b). The subspecies *H. pileatus atricapillus,* also basically a Caatingas bird where it is sympatric to the nominate form, spreads further west into Maranhão in perhaps deciduous formations related to the 'sertão', south to the Planalto in Minas Gerais and São Paulo, and southwest in calcareous mesophilous forests in Goiás and Federal District (Silva, 1989). Further west it reaches the Corumbá area and E Paraguay, and also extends to the Serranías of Chiquitos, Santa Cruz de la Sierra, and the deciduous forests in the Subandean piedmont in NW Argentina. The Urubamba and Marañón valleys in Peru comprise the few known collections of the subspecies *H. pileatus motacilloides* (Cory & Hellmayr, 1924). There is thus a conspicuous similarity between the pattern of distribution of the polytypic Formicariidae *Herpsilochmus pileatus* and some woody species such as *Anadenanthera colubrina* var. *cebil* , *Astronium urundeuva* or *Pterogyne nitens* , outstanding members of what is called here Residual Pleistocenic Seasonal Formations Arc (see Sect. 5.3.1).

The whole of the genus *Melanopareia* in the Rhinocryptidae seems to have this distribution (Fig. 7.11), in which case it would be endemic to the Pleistocenic Arc. The nominate form of *Melanopareia torquata* covers a rather reduced sector of the caatingas, while the subspecies *rufescens* and *bitorquata* link NE Brazil to the Planalto in

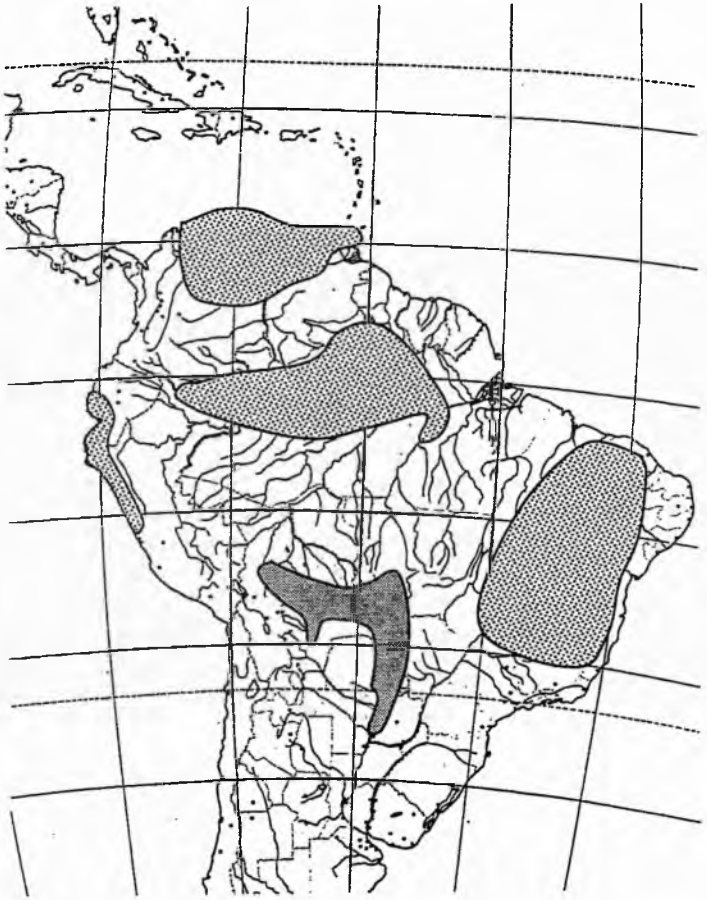


Fig. 7.9: Distribution map of *Icterus icterus* (*I. i. strictifrons* : more densely stippled).

Fig. 7.10: Distribution map of *Herpsilochmus pileatus pileatus* (diamonds), *H. p. atricapillus* (dots) and *H. p. motacilloides* (stars).

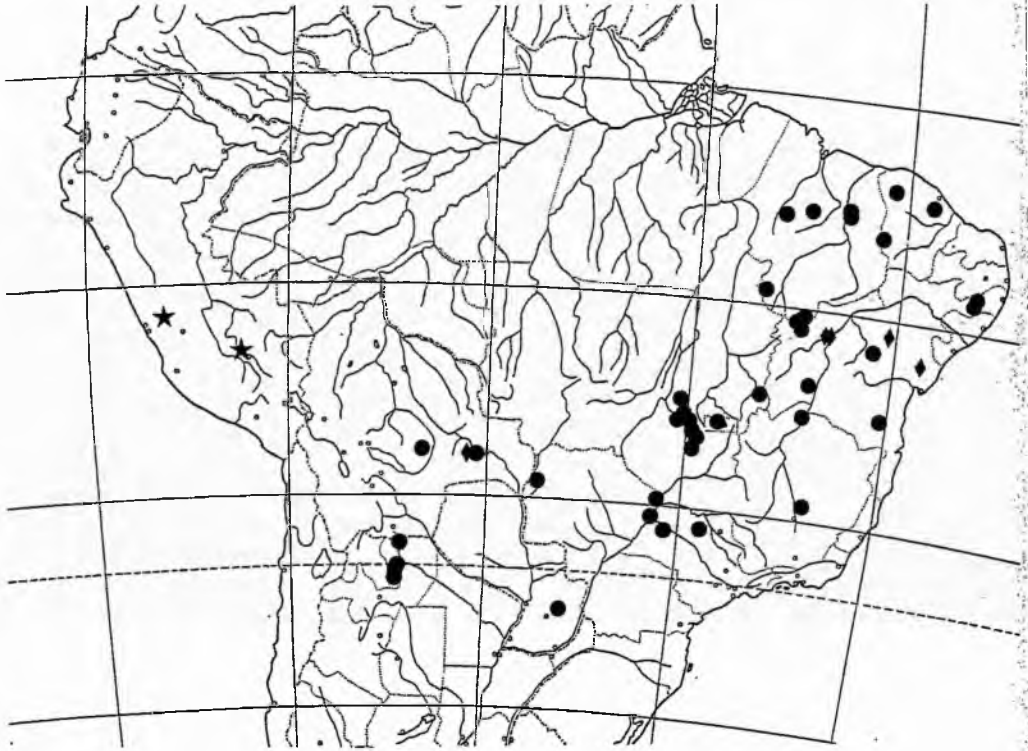


Fig. 7.11: Distribution map of the genus *Melanopareia* : *M. torquata torquata* (open squares), *M. t. rufescens* (diamonds), *M. t. bitorquata* (diamond in squares); *M. maximiliani maximiliani* (open circles), *M. m. argentina* (dots); *M. elegans* (stars); *M. maranonica* (triangles).

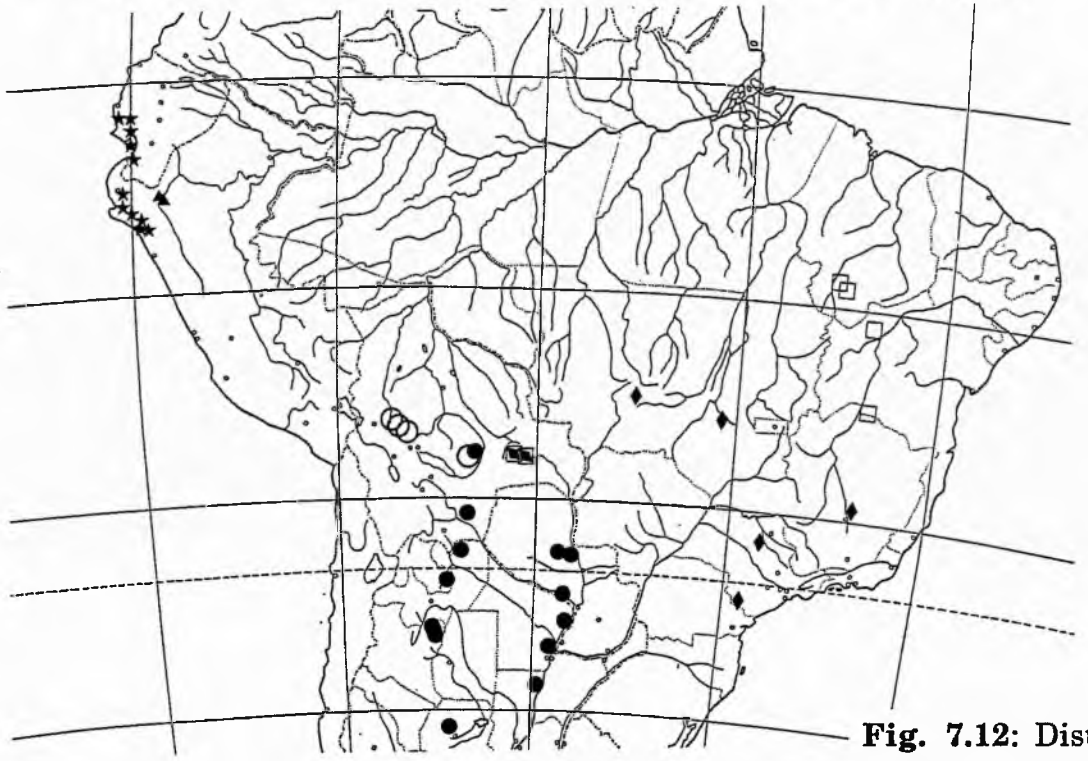


Fig. 7.12: Distribution map of *Contopus cinereus cinereus* (diagonal pattern), *C. c. pallescens* (vertical hatching) and *C. c. brachytarsus* (stippled).

São Paulo and isolated areas in Goiás and Mato Grosso, and to the Chiquitos sector in Bolivia respectively. *Melanopareia maximiliani argentina* shows a typical amphichaquenian distribution, sticking to the Paraguay-Paraná system on the east, and to piedmont areas from Santa Cruz de la Sierra to Córdoba, in the west; the nominate *maximiliani* spreads only in central Bolivia. Finally, *M. elegans* is restricted to SW Ecuador and NW Peru, while *M. maranonica* seems to be an endemic of the neighbouring dry valley of the lower Marañón river.

Another species listed by Short but not considered chaquenian here is the Tyranniidae *Contopus cinereus* , with the nominate form in SE Brazil, Misiones and E Paraguay, whilst *C. cinereus pallescens* spreads from the Caatingas through central Brazil to the Subandean piedmont in Bolivia and Argentina (Fig. 7.12). Another subspecies, *brachytarsus* , on the other hand, shows disjunct populations in the Guianas, Amazonian Venezuela, SW Ecuador and NW Peru area connected to the Marañón valley, the dry Caribbean coast of Venezuela and Colombia spreading south via the Magdalena river valley, and then into Central America. The euphonic Icteridae *Gnorimopsar chopi* is also what is here regarded as an amphichaquenian species (see also Olrog, 1963a, p. 24), though frequent in the Eastern Chaco of Paraguay and Argentina. Its subspecies *sulcirostris* shows an exciting disjunction between the Brazilian Caatingas and the Subandean Piedmont Forests in S Bolivia and NW Argentina (Fig. 7.13), thus closely paralleling the distribution of the tree *Piptadenia viridiflora* (see Fig. 5.48). Amphichaquenian as well is the Tyranniidae *Inezia inornata* (Fig. 7.14), whose closest ally (*I. tenuirostris*) occurs in the driest areas of Colombia and Venezuela Caribbean coast. The parakeet *Aratinga nenday* (also referred to the monotypic genus *Nandayus*) is clearly restricted to the major river valleys and to the axis Santa Cruz-Corumbá (Fig. 7.15), thus bordering the Chaco but not getting into it and coinciding with the Pleistocenic Arc in its 2nd nucleus (see Sect. 5.3.1); the latter pattern of distribution seems to be closely followed by another monotypic genus and species in the Tyranniidae, *Culicivora caudacuta* (Olrog, 1963a; Meyer de Schauensee, 1966; Fitzpatrick, 1980). There must also be a number of species which were not cited by Short for the Chaco but which follow the Pleistocenic Arc. Such is the case of *Formicivora melanogaster* (Fig. 7.16), mapped from data in Cory & Hellmayr (1924).

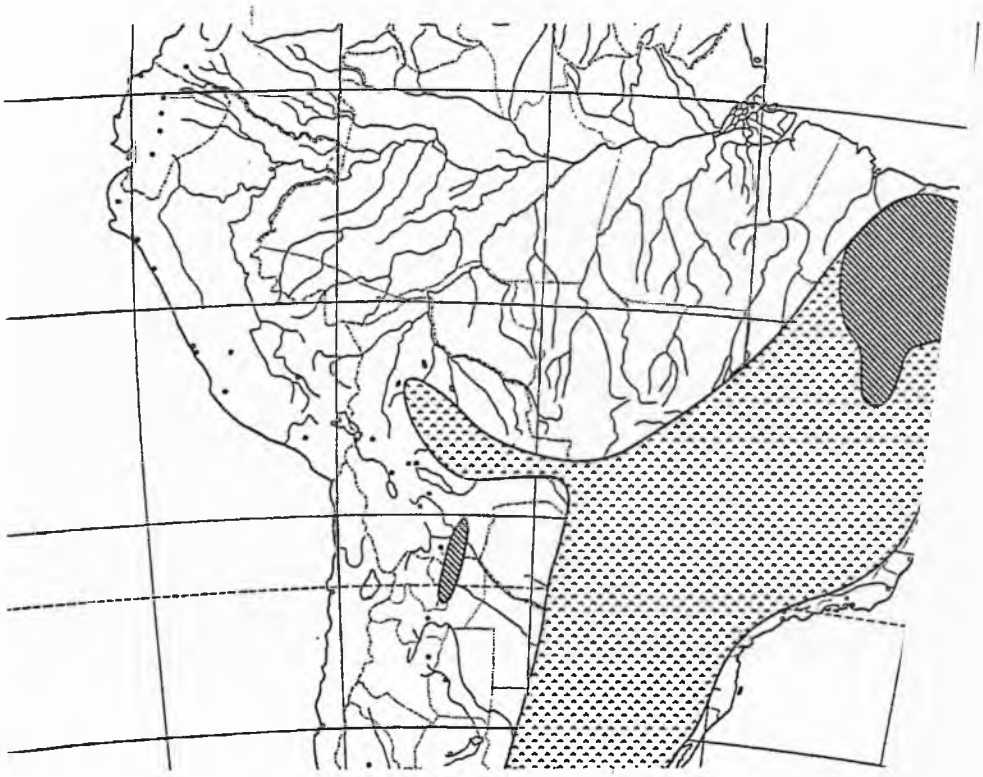


Fig. 7.13: Distribution map of *Gnorimopsar chopi chopi* (stippled) and *G. c. sulcirostris* (oblique hatching).

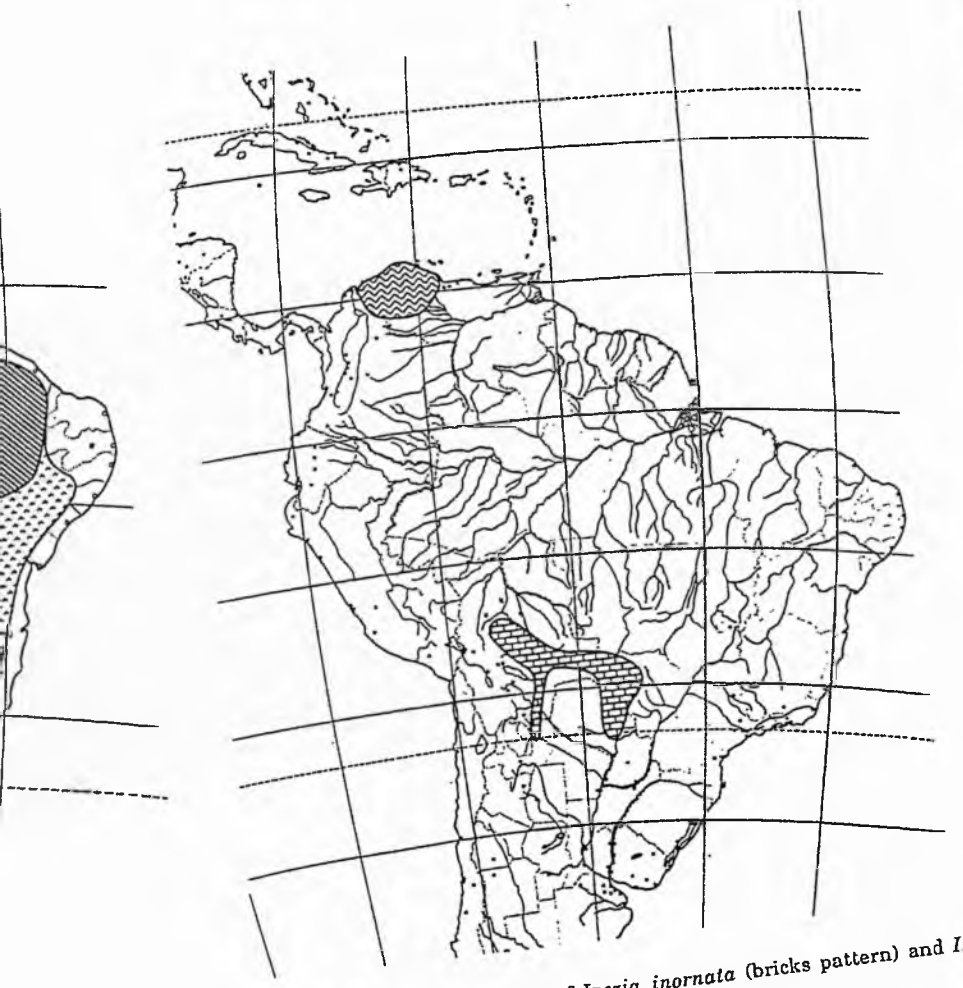


Fig. 7.14: Distribution map of *Inezia inornata* (bricks pattern) and *I. tenuirostris* (wavy pattern).

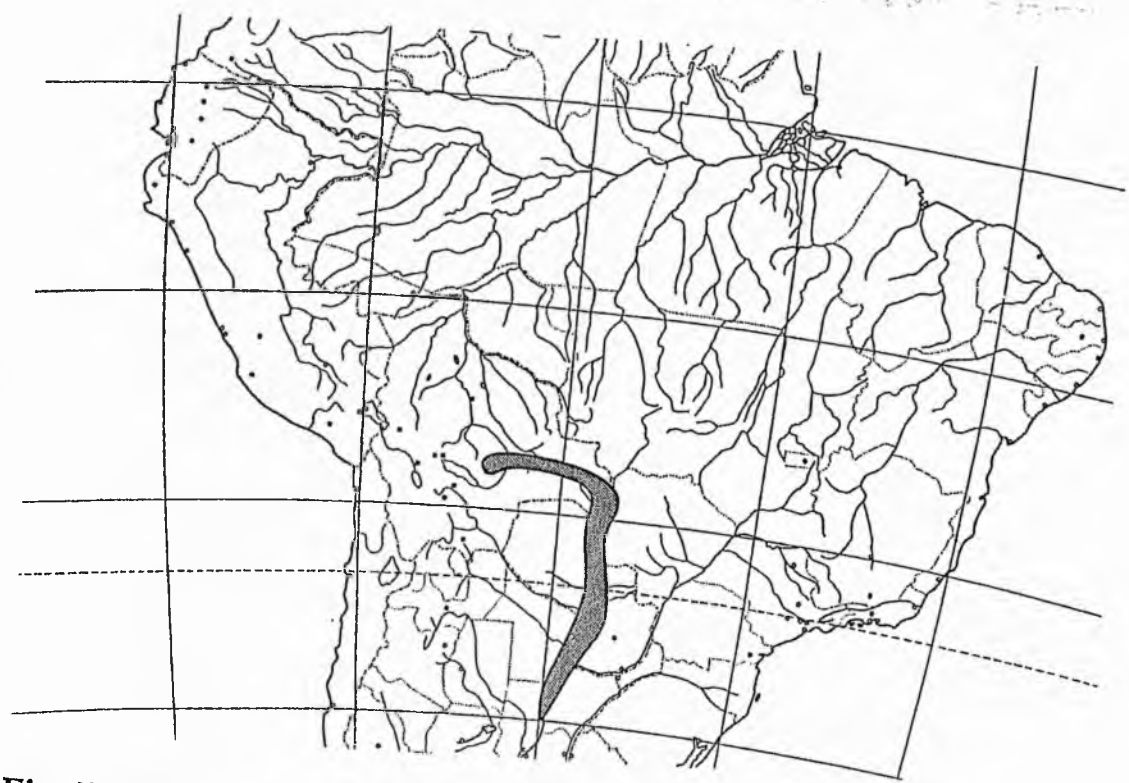
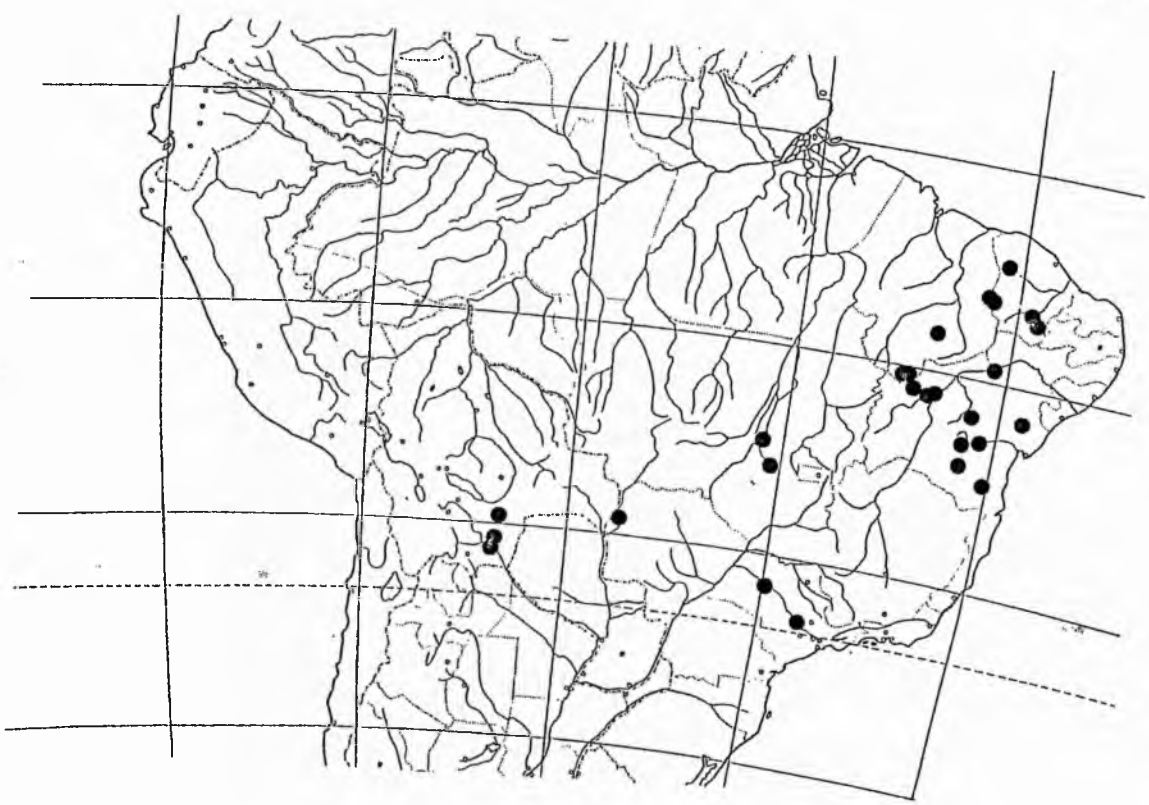


Fig. 7.15: Distribution map of *Nandayus* [*Aratinga*] *nenday*.

Fig. 7.16: Distribution map of *Formicivora melanogaster* (both *melanogaster* and *bahiae* forms).



The close relationship between the Caatingas and the dry SW Ecuador-NW Peru vegetation, already pointed out in Ch. 5, can be emphasized by the range of the Furnariidae *Fluvicola nengeta* (Fig. 7.17), whose nominate form covers the Brazilian NE (Vaurie, 1980) while subspecies *atripennis* occurs exclusively on the other side of the continent in the aforementioned area. The even closer links, from the phytogeographical point of view, between the Caatingas and the dry Caribbean sector in northern South America is illustrated by *Spinus yarrellii* (Fringillidae) in Fig. 7.18, erroneously regarded as a Caatinga endemic by Müller (1973, p.115). This case is paralleled by the Caatingas' endemic *Phylloscartes roquettei* , known only from arboreal caatinga in the Januária area (Silva, 1989), whose closest relative *P. flaviventris* occurs sympatrically with *Spinus yarrellii* in northern Venezuela, plus an isolated collection in Peru in, presumably, dry Andean valleys.

Numerous other examples of bird species following the patterns of plant distributions presented in this thesis can be found in the literature. Vaurie's (1980) monograph on the Furnariidae shows several cases, such as that of *Furnarius figulus* (see his map 5) which clearly links the Caatingas to the central Amazonian area around Santarem in Pará, and *Furnarius leucopus* (same map) with three disjunct populations in NW Venezuela and N Colombia (surrounding the lake Maracaibo), in SW Ecuador-NW Peru, and then a wider distribution from the Guianas and Rio Branco in Brazil to central Amazon valley and west of Obidos, south to Bolivia and central Mato Grosso, to finally reach the Caatingas. The whole of Vaurie's *Synallaxis* group 4 seems to be confined to the Amphitropical Seasonal Forests pattern of distribution (see his map 15 vis-à-vis Sect. 5.3.3), with *S. erythrothorax* in Yucatán, Tehuantepec and Guatemala, *S. candei* and *S. cinnamomea* in dry coastal Colombia and Venezuela, *S. gularis* in Andean valleys of Colombia, Ecuador and Peru, and therefore linking with *S. stictothorax* of SW Ecuador-NW Peru, *S. kollari* isolated in Rio Branco (where one of the most typical caatinga tree species, *Commiphora leptophloeos* , Fig. 5.35, has been collected), and finally *S. scutata* which spreads from the Caatingas to the Subandean piedmont through the Cerrados and mesophilous forests within the latter savannas (Silva, 1989). *Certhiaxis*

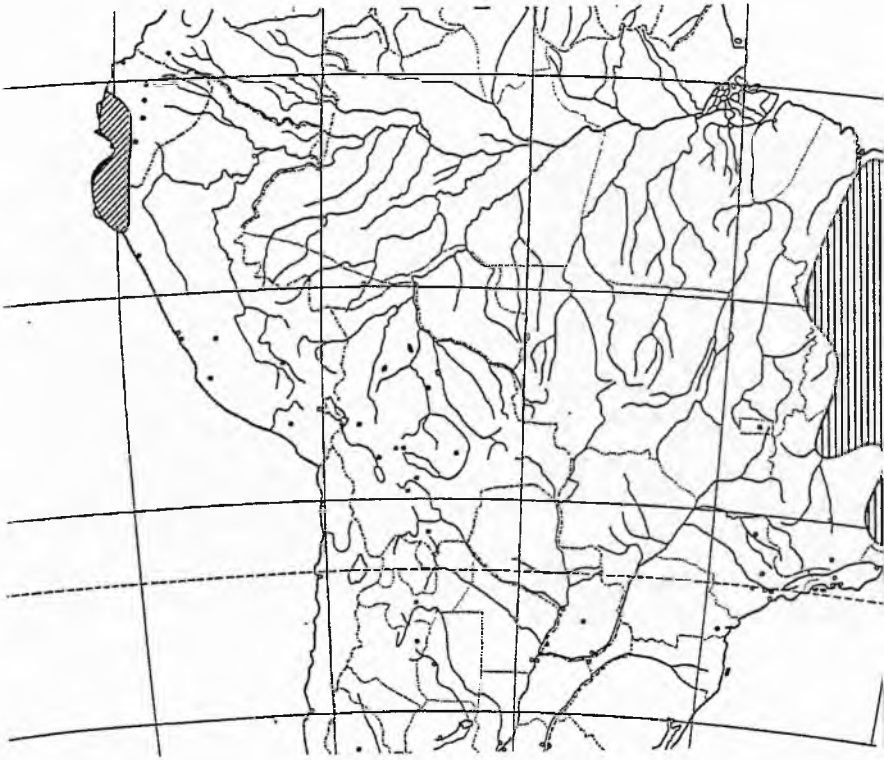


Fig. 7.17: Distribution map of *Fluvicola nengeta nengeta* (vertical hatching) and *F. n. atripennis* (oblique hatching).

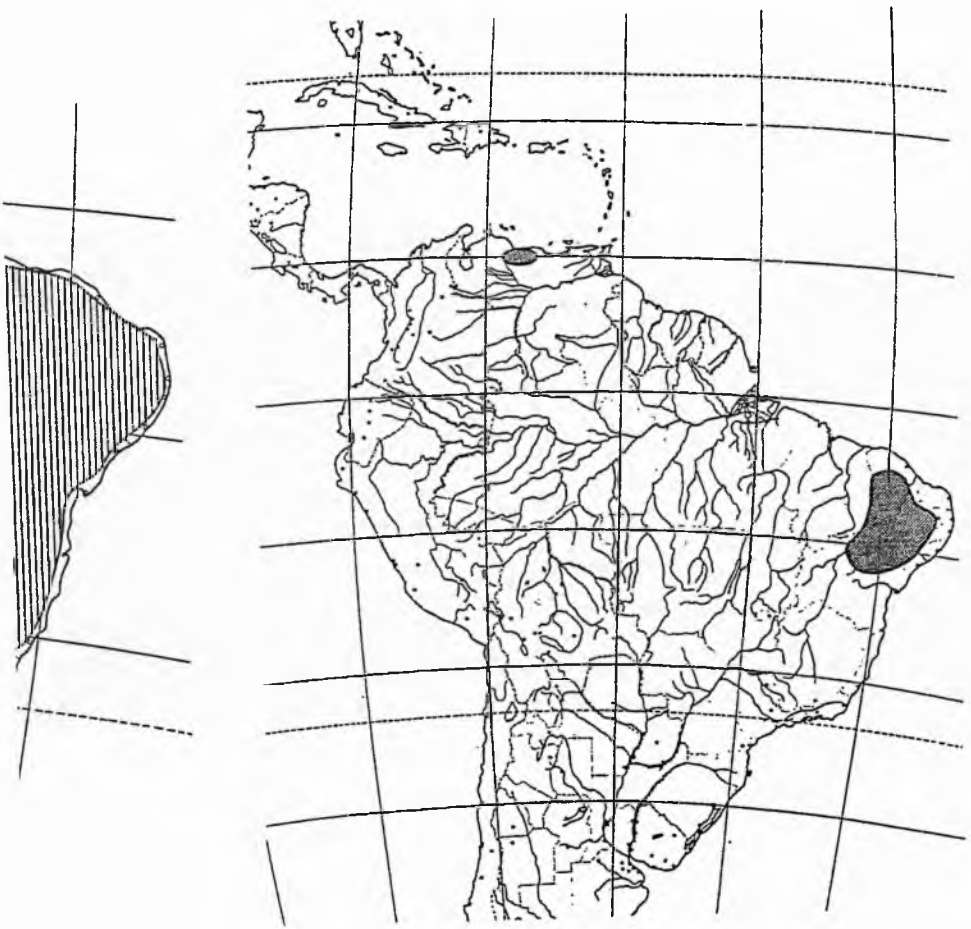


Fig. 7.18: Distribution map of *Spinus yarrellii*.

(=*Cranioleuca*) *semicinerea* would be a caatinga endemic but for some isolates in south central Goiás (Vaurie, 1980; Teixeira & Luigi, 1989). From Short's work (1975) some few other examples can be extracted, such as the Corvidae superspecies *Cyanocorax chrysops* or the Trochilidae *Phæthornis pretrei* , which link the Subandean piedmont in NW Argentina to the Caatingas. However, an exhaustive analysis of avian distribution is beyond the scope of this thesis.

7.3- The mammalian evidence:

The mammalian fauna of South America can shed further light onto the nature of the relationship of the two regions under study. The Caatingas mammals have been studied and listed by Mares et al. (1981b), Mares et al. (1985) and updated by Willig & Mares (1989), who found *Kerodon rupestris* as the only endemic of the region. They consider the Caatingas mammals essentially a subset of the cerrado fauna (Mares et al., 1985), with the paradoxical situation of a largely mesic-adapted tropical fauna in an area distinctive for its aridity and drought-adapted flora. The Chaco mammals have been more extensively studied (Massoia, 1970; Wetzel & Lovett, 1974; Myers & Wetzel, 1979 & 1983; Bucher, 1980; Mares et al., 1981a; Myers, 1982; Mayer & Brandt, 1982), and seem to show a higher degree of endemicity. The Chaco has the peccary with the most restricted distribution, the monotypic *Catagonus wagneri* (Wetzel et al., 1975; Sowls, 1980-83; Mayer & Brandt, 1982), and several endemic rodent species (Müller, 1973; Myers, 1982). No endemic bats to the Chaco are known to occur to date, and its bat fauna appears to result more from the deletion of species from neighbouring areas, rather than from the differentiation or incorporation of new elements (Myers & Wetzel, 1983).

Thus, although some comparative studies of South American mammalian faunas suggest a strong affinity between the Chaco and Caatingas dispersal centres, e.g. Müller (1973), once again an analysis of individual cases provides a different picture. The excellent studies by Michael Mares and collaborators (Mares et al., 1981a & b), both in a central area of the Caatingas in Pernambuco (Brazil) and in the Chaco of E Salta (Argentina), provide extensive mammal lists with detailed habitat comments. It is particularly important that these authors studied not only the animal communities of reference, but also those of

neighbouring (Puna, Prepuna, Yungas and Subandean Piedmont Forests) and enclosed formations (such as the cerrado of the Chapada do Araripe). A comparison of the lists indicates that the dry deciduous forests of the Subandean piedmont (so-called Transitional Forests) holds six species and two genera in common with the Caatingas, but these are absent from the Chaco. In contrast, only one of the species in common between Chaco and Caatingas is also absent from the Piedmont Forests (*Euphractes sexcinctus*). These results confirm the pattern that has emerged for birds and tree species, i.e. that there is a strong floristic and faunistic link between the Caatingas and the narrow fringe of deciduous subtropical forests in NW Argentina and SW Bolivia, but not with the main Chaco area.

The Chiropteran fauna of the Paraguayan Chaco was analyzed by Myers & Wetzel (1983), with comparative listings between the Chaco Boreal and several South American biomes: Venezuela, Surinam and Guianas as one single block, Amazonian Peru, Bolivia, Caatingas, SE Brazil (basically the coastal states from Rio de Janeiro to Rio Grande do Sul), E Paraguay, and Uruguay. They reckoned the number of species in common of each of these biomes with the Chaco Boreal, and the Simpson's index of faunal resemblance was calculated. In all likelihood they were expecting to find a high similarity between Chaco and Caatingas, but these two regions rendered the second lowest number of species in common (Uruguay was the lowest), and the lowest similarity index. The highest similarities for the Chaco were found with neighbouring eastern Paraguay and the Venezuela-Guianas block. Myers & Wetzel (op . cit .) blamed sampling techniques for this result: "The stronger relationship between Chacoan and Venezuelan faunas than between Chacoan and NE Brazilian faunas, for example, is probably an artifact of incomplete sampling". This statement merits two comments: firstly, whatever sampling errors may exist, they are likely to be of little impact compared with the attempt by these authors to compare faunas of well-defined natural biomes, such as the Chaco, Caatingas, Amazonian Peru or what they called SE Brazil, with those of political areas such as Bolivia and Uruguay, or a concoction of different environments such as those included under the heading 'Venezuela' (which involves some West Indies as well, and ranging ecologically from tropical rainforests to the Caribbean semidesert). Secondly, the quoted

sentence reveals the deep-rooted prejudice evident in many South American biogeographical studies that a strong relationship between Chaco and Caatingas must exist, even when their own data indicates otherwise. Furthermore, a number of the bat species regarded by Myers & Wetzel (1983) as chaquenian have never, in fact, been seen or collected in Chaco proper but only in marginal areas here not regarded as Chaco s.s. (as it happens with a number of avian species listed by Short, 1975): *Peropteryx macrotis* , *Phyllostomus hastatus* , *Glossophaga soricina* , *Carollia perspicillata* , *Sturnina lilium* , *Vampyrops dorsalis* , *V. lineatus* , *Artibeus lituratus* , *Tadarida macrotis* . Since several of these species are members of the Caatingas volant mammals fauna, their exclusion from the Chaco weakens even more the links between the regions.

The bat species *Lonchophylla mordax* , a caatinga element (Willig & Mares, 1989), follows to a certain extent some of the distributional patterns described in previous sections, such as that of the bird *Fluvicola nengeta* (Fig. 7.17) or those of some of the trees included in Ch 5.3.2, e.g. the *Geoffroea striata/spinosa* complex (Fig. 5.58). It occurs in S Central America, W Colombia (probably in dry interandean valleys), dry coastal E Ecuador and NW Peru, to then reappear in the east of Brazil including the Caatingas (Koopman, 1981, Fig. 10, & 1982). Except for an specimen from Belém, Pará, it has not been recorded for the Amazon.

7.4- Herpetological distribution and other sources of evidence:

It is very difficult to draw conclusions from alleged herpetological relationship between Chaco and Caatingas. Vanzolini has repeateadly stated that much more collecting is needed and taxonomical studies are required to fully understand the herpetofauna distribution in South America (Vanzolini, 1970 & 1974). The degree of endemicity of the Chaco, although a very contentious matter – compare Müller (1973, pp. 143-145), to Blair (1976), Gallardo (1979), and Bucher (1980) – seems to be much higher than that of the Caatingas. Tropical forms penetrate along the western and eastern boundaries of the Chaco via gallery forests, such as *Iguana iguana* and *Anolis chrysolepis* , overlapping sometimes with true chaquenian elements and motivating some authors to include very different entities as faunal elements of the region, as already emphasized by Müller (op .cit .). Basically, however,

endemic elements of the Chaco are at least one monotypic genus, *Chacophrys* (Müller, op .cit .), and some species such as *Tropidurus melanopleurus* , *Liolæmus chacoensis* (Müller, op . cit .), and *Leptodactylus laticeps* (Bucher, 1980). The Caatingas have apparently only one endemic lizard, *Tropidurus semitæniatus* , so that there is no lizard fauna characteristic of the region but it is simply part of the so-called diagonal of open formations extending from Maranhão to NW Argentina (Vanzolini, 1970, 1974 & 1976). This would imply that there should be strong affinities between Chaco and Caatingas by way of the central Brazilian Cerrados, as shown by *Phyllopezus pollicaris* and *Gymnophthalmus multisculatus* vs. *G. rubricauda* (Vanzolini, 1974). However, Duellman's (1979) analysis at familial level of the South American herpetofauna renders little evidence for such a link; his Brazilian Shield ecophysiographic region (lumping together Cerrados and Caatingas) has 31 families in common with the Atlantic Forest and with the Guianas Shield, 27 with the Caribbean-Orinoco area, and only 20 with the Chaco. Analyzing only the data for the Caribbean-Orinoco area, the Brazilian Shield and Chaco, there are eight families in common between the two first regions which are absent from the Chaco, while only three are absent from the Brazilian Shield but common to Chaco and the Caribbean sector (Duellman, 1979). These data seem to indicate a somewhat stronger relationship between the Caribbean-Orinoco area and the Brazilian Shield, than between the latter with the Chaco.

Finally, the Caatingas as a biogeographical province seem to be very well defined also by their scorpion fauna: there are at least five endemic species (Lourenço, 1990). The nine species of the scorpion genus *Rhopalurus* provide additional information of the actual Caatingas links (Lourenço & Sastre, 1988). Apart from three endemisms in the West Indies, there are four species in the Caatingas (*R. agamemmon* , *R. acromelas* , *R. debilis* , *R. rochae*), two of which also occur in the Cerrados, another one is endemic to campos around Santarém, Pará (*R. amazonicus* ; Lourenço, 1986), and the last one, *R. laticauda* , is distributed in the dry Caribbean sector of Colombia and Venezuela plus the Llanos in both countries, with one subspecies in the Guianas. Once again the evidence suggest a great affinity Caatingas-Caribbean dry area via Amazonia – and Guianas – isolated disjunctions, rather than the Chaco-Caatingas links postulated by Lourenço (1990).

Cladistic analysis performed by Lourenço & Sastre (1988) indicates that *R. amazonicus* is in an intermediate taxonomic position between the Caribbean species and two of those from the Caatingas that spread to the Cerrados (*R. agamemmon* , *R. acromelas*), whereas the other two caatinga species are closer to the West Indies endemics. Lourenço & Sastre (1988) regard *R. amazonicus* as a vestige of an ancient continuous distribution of the genus across the lower Amazon river valley.

8. DISCUSSION

In any study of floristic links such as that between Chaco and Caatingas vegetation in South America there is an underlying dilemma: vicariance or dispersal?. That is, are present-day distribution patterns the result of a previously continuous expanse, later interrupted, or are they simply the consequence of propagule dispersal which have found propitious terrain in areas with seasonal climate?. Harley (unpubl. mscrp.), in a study of 'campo rupestre' floristics in SE Brazil which emphasized the links to the Mesa and Tepui formations in Venezuela, suggested that the number of species in common is too high to suppose that mechanisms of long-distance dispersal could have acted in this case, and argued that there must have been an earlier physical connection. This reasoning, which could be certainly applied here, lies at the core of the 'vicariance' argument. Whilst occasional 'unusual' distributions may be the consequence of chance long-distance dispersal effects, repeated distributions of taxa in a similar pattern give support to a vicariance explanation. The recurrent occurrence of a disjunct distribution outline, or endemisms whose closest relatives are vicariant in other segments of the same disjunct distribution pattern, provide a firm conviction that a common event (or events), a common migration pathway, a common expansion-regression phenomenon has taken place. This view finds further support in the fact that plant taxa following these patterns come from widely different families, phylogenetically very distant in most cases; that the patterns can also be found repeated in animal distribution cases (Ch. 7) and when the latter are bird species, those that follow the particular distribution patterns studied here are non-migratory and some of them virtually non-flying taxa.

8.1- Redefinition of the Chaco province:

Attention has been drawn for some time to the physiognomic, floristic and faunistic connections between the Caatingas of NE Brazil and the Gran Chaco region of Bolivia, Paraguay and Argentina, an established view that has prevailed unchallenged so far. In studying this problem the need of a thorough analysis of the present-day notion of the Chaco arose. In the literature available to date the concept of the Chaco as a phytogeographical province has simply been equated with the Chaco as a geographical region. However, the comparative study and

phytosociological analyses undertaken here show that the geographical region known as the 'Gran Chaco' in fact includes rather different kinds of vegetation. Such analyses then provide the basis for an attempt to redefine the 'Chaco proper'.

In Sect. 6.1 the results of three different types of analysis applied to the Gran Chaco vegetation have been presented : the classical phytosociological approach and, as a more objective yardstick to evaluate this, two numerical analyses were performed, one to classify (CLINK) and one to ordinate (PCA) the samples. The congruence between the different results is striking. Out of the 23 vegetation units that had been regarded as chaquenian by different authors (see Ch. 2 & Table 6.1), five are definitely non-chaquenian (Gallery Forest, 'Selva de Ribera', 'Tipa-Pacará' Forest, 'Palo blanco' Forest, and Calcareous Forest), four are here considered transitional with neighbouring formations (the Austro-Brazilian Transitional Forest and three of the communities of Mato Grosso do Sul), and 14 correspond to what is here defined as Chaco *sensu stricto* : the four 'Quebrachales', 'Palosantal', 'Algarrobal', 'Vinalar', 'Cardonal', the two 'Palmares', both Sierra Chaco, the Arid Chaco Woodland and the Chaco Forest at Pto Murtinho. A brief discussion on the excluded communities follows.

(a) Excluded communities:

Between the communities listed in Table 6.1, none of the Gallery Forest (**A**), 'Selva de Ribera' (**B**), 'Tipa-Pacará' Forest (**C**), 'Palo blanco' Forest (**D**) and the Calcareous Forest of Mato Grosso do Sul (**F**) can be regarded as chaquenian in character. Climate, soils and water regime are entirely different from that which prevails in the Chaco *s.s.*, and as a result their flora is essentially of Amazonian lineage (*sensu* Cabrera & Willink, 1980). All of these vegetation types are well defined, each characterized by a floristic group comprising the species which are exclusive to them within the scope of this study. Moreover, the numerical analyses (Figs 6.1 & 6.2) have shown that they are more closely inter-related, and linked to what has been called in the present study 'Austro-Brazilian Transitional Forest', than to the Chaco *s.s.* communities. Therefore, none of these five vegetation types should be included in the Chaco phytogeographical province.

(b) Transitional communities:

The four transitional units consist of three from the Mato Grosso do Sul area studied by Prado et al. (in press b): the *Schinopsis balansae* parkland (**G**), the *Aspidosperma-Mimosa* scrubland (**H**), and the *Diplokeleba-Tabebuia-Capparis* scrubland (**I**), and finally the here-named 'Austro-Brazilian Transitional Forest' (**E**). The first three communities contain a very low percentage of true Chaco species (Prado et al., in press b), along with a number of cerrado and semi-deciduous forest elements, and none of the three can be fully ascribed to any of the major phytogeographical units which converge in the Pantanal, i.e. Cerrados, Amazonian, Paranense and Chaco provinces (Adámoli, 1982). Furthermore, the numerical analyses (Fig. 6.2) show these communities in a clear transitional position between the Chaco *s.s.*, and the wetter vegetation units.

The Austro-Brazilian Transitional Forest (**E**) is undoubtedly the climax community in the east of the Gran Chaco area (Lewis & Pire, 1981, *sub* 'bosque chaqueño'), i.e. the sector referred to as 'Eastern Chaco' in all phytogeographical classifications (Morello & Adámoli, 1968; Ragonese & Castiglioni, 1970; Cabrera, 1971 & 1976). Four true Chaco communities also manage to extend into this eastern area. These are the *Schinopsis balansae* 'quebrachal' (**K**), *Prosopis* spp. 'algarrobales' (**P**), *Copernicia australis* 'palmares' (**S**), and *Stetsonia coryne* 'cardonales' (see Sect. 2.3.7.b). They are evidently edaphic-dependent, and their presence in an area of over 900 mm yearly rainfall is allowed only by the physiological drought caused by the high salt content of the soil and consequent higher osmotic potential. Consequently, and contrary to the position sustained by Ragonese & Castiglioni (1970) and Cabrera (1976), the 'quebrachal' of *Schinopsis balansae* should not be regarded as a climax community, since rather it thrives on non-climatogenic saline soils, with high clay level, periodical waterlogging, elevated Na^{++} concentration and very strongly alkaline subsoils (Espino et al., 1983). Thus, true Chaco vegetation is found in a strip of some 100 km wide, parallel to the Paraguay and Paraná rivers, in an area where climatic, edaphic

and geomorphological conditions are different from those in the center and west of the Gran Chaco. Presumably, the salinity factor is responsible for this outlying representation, since Chaco elements can survive in edaphic conditions which are hostile for the subtropical humid forests species of the Austro-Brazilian Transitional Forest. This hypothesis is exactly the opposite to Hueck's (1972), who postulated that chaquenian species would occur on higher, drier ground within the floodable, water-modelled Eastern Chaco. On the contrary, such drier areas are covered by a different kind of forest dominated by species such as *Patagonula americana* , *Phytolacca dioica* , *Ruprechtia laxiflora* , *Gleditsia amorphoides* , *Tabebuia impetiginosa* , *Pisonia zapallo* , and *Enterolobium contortisiliquum* . All of these species occur elsewhere in subtropical humid forests in S Brazil, E Paraguay and N Argentina. Indeed, the species listed above are all widespread in South American forests, and extend to NE Brazil or humid Atlantic forests (Klein, 1967), or even to Central America and Mexico in similar ecosystems (*Tabebuia impetiginosa* , in Gentry, 1979).

Most species of the Austro-Brazilian Transitional Forest are elements which are common to the five vegetation types here excluded altogether from the Chaco *s.s.*, e.g. the species listed above together with *Diplokeleba floribunda* , *Astronium balansae* , *Chrysophyllum gonocarpum* , *Pithecellobium scalare* or *Brunfelsia australis* (see Table 6.1). Seven of the most typical Chaco species[1] can also appear in this transitional unit, but they are never dominant trees and seem to be at the extreme of their ecological range in this area. Hardly any of these chaquenian intruders can be found further east in wetter areas either in Argentina, Paraguay or Brazil, and it is likely that their existence in this unit could be due to anthropogenic alteration of the environment (overgrazing, selective felling), or even brought in by cattle. Therefore it is proposed that this vegetation type, which has

[1] These are: *Geoffroea decorticans* , *Aspidosperma quebracho-blanco* , *Ziziphus mistol* , *Prosopis nigra* , *Schinus fasciculatus* , *Acacia praecox* and *Caesalpinia paraguariensis* (see Table 6.1, FG XXII). Sometimes even *Schinopsis balansae* may appear in this forest, but its occurrence is very occas ional and marginal to the unit (Lewis, J.P., *in litt.*).

received several different names by different authors, and has generally been included in the Chaco province (Cabrera, 1971 & 1976), is better called **Austro-Brazilian Transitional Forest** and should be excluded altogether from the Chaco *s.s.* .

This forest is basically a very impoverished version of the Brazilian Subtropical Forests (*sensu* Andrade-Lima, 1966a, and Klein, 1972), which is here at the extreme western limit of its distribution. Furthermore, and despite the presence of some chaquenian elements in it, the Austro-Brazilian Transitional Forest should be regarded as a component of the Paranense province of the Amazonian Dominium (*sensu* Cabrera & Willink, 1980), since the dominant trees are species which are mainly distributed in other districts of this province where, however, they may be of lesser importance. Thus, of the Paranense province floristic stock, these species are probably those that can tolerate a few frosts each year, and can still compete successfully in areas with less alkaline and less waterlogged soils against the chaquenian species pushing east.

This interpretation is reinforced by the fact that most of the dominant species of the Austro-Brazilian Transitional Forest reappear further west, jumping over 700 km of dry Chaco plains, in the Yungas province (Smith, 1962; Ragonese & Castiglioni, 1970; Cabrera, 1976) in the 'Tipa-Pacará' (**C**) and 'Palo blanco' (**D**) Forests. There is a very close relationship between those three vegetation units, as shown by several floristic groups of Table 6.1 and strongly supported by the numerical analysis. However, although units **C** & **D** also include some widespread chaquenian species, it is of interest that few authors tried to include these two forest types in the Chaco (e.g. Hueck, 1972), whilst virtually all phytogeographers have merged without hesitation the Austro-Brazilian Transitional Forest with the Chaco, with perhaps the sole exception of Castellanos & Pérez-Moreau (1944) in their map of vegetation of Argentina.

The fact that the so-called 'Eastern Chaco' is in effect a meeting point of quite diverse floristic elements, i.e. true xerophytic

chaquenian communities and humid subtropical and tropical species, has been perceived by some previous authors. Thus, Cabrera (1970) was aware that the boundary between the Chaquenian and Amazonian Dominia, which meet in the Eastern Chaco, is confused, and he remarked that the whole of the river Paraguay basin is an immense transition area with a very complicated intermingled pattern. A striking example of such intermingling is that the current concept of 'Eastern Chaco' even includes 'paratodales' of *Tabebuia caraiba* in floodable localities associated with the river Pilcomayo valley in SE Paraguayan Chaco region and NE Formosa in Argentina (Chodat & Vischer, 1977; Fiebrig, 1933; Ragonese & Castiglioni, 1970; Morello & Adámoli, 1974, p.42). *T. caraiba* can hardly be accepted as Chaco species (see map 5.52) since it also occurs in NE Brazil in the 'sertão' and 'agreste' (Andrade-Lima, 1960 & 1989), is also an abundant species in the Cerrados (Heringer et al., 1977; Furley & Ratter, 1988; Ratter et al., 1988a), and the 'paratodales' are one of the main features of the Pantanal landscape (Ratter, 1984; Allem & Valls, 1987)!.

Although edaphic factors can explain the eastward expansion of some Chaco taxa, the reason why southern or central Brazilian hygrophilous elements can expand westwards to interdigitate with chaquenian communities must be climatic. In Chaco vegetation maps the line drawn to separate the so-called 'Eastern Chaco' from the rest of the province (see Fig. 2.1; also Hueck & Seibert, 1981) seems to coincide roughly with a rainfall isoline somewhere between 950 to 1000 mm per year (see Fig. 2.4), and also with the alleged limit between humid and dry climates, the MI(Moisture Index)=1 line (Box, 1986). In Ragonese & Castiglioni's map (1970), where their concept of 'Eastern Chaco' covers the eastern half of the Gran Chaco region, this line coincides roughly with the western boundary of the 'Pilaguense' and 'Bosque Chaqueño' districts.

The climate classification systems of Koeppen and the two systems proposed by Thornthwaite have been compared for Argentina by Burgos & Vidal (1951), who concluded that Thornthwaite's 2nd System is the most fitted to the distribution of the natural vegetation. For the Argentine Chaco, this correlation is very good : the transitional belt proposed here (Fig. 8.2) matches very well with an equivalent narrow

band along the river Paraná with C_2B_4'ra' climate (Fig. 8.1), and so does the zero isoline for the MI according to Thornthwaite's 2nd System (Burgos & Vidal, 1951, Fig.7 D). The similarities extend even to most of the chaquenian districts proposed by Ragonese & Castiglioni (1970), such as the Pilaguense, Matacense, and Santiagueño districts, to which the corresponding climate types are C_1A'da', DA'da' and DB_4'da' respectively, and the districts Campestre, Mixed Forests & Savannas and Chaquenian Forest as a group with the corresponding climate type C_1B_3'da'. It is noteworthy that a very similar kind of climate to that of the eastern Transitional Belt appears to the west of the Chaco in areas occupied by both the 'Tipa-Pacará' and 'Palo blanco' Forests!.

Given the weight of floristic and correlated climatic and edaphic evidence, the question could be posed now why the 'Eastern Chaco' has traditionally been considered as truly chaquenian, as in Morello & Adámoli (1968), Ragonese & Castiglioni (1970), Cabrera (1976), Hueck & Seibert (1981), and Ramella & Spichiger (1989). The reasons are more historical than botanical. The rainforests or thorny dry woodlands formed a barrier to an eastward expansion for centuries with the result that most of the exsiccata collected on the eastern side of the Paraná and Paraguay rivers have simply the locality 'Chaco', whether they are xerophytic or humid forest species, just because the collector ferried the river or sailed along the tributaries. The NE Argentine Chaco region and the Paraguayan Chaco region were cautiously explored by naturalists in a narrow fringe parallel to the big rivers or their tributaries, mainly the Pilcomayo (see the picturesque account by Kerr, 1968), at the beginning of this century. Hochreutiner (1923) remarked that the Paraguayan Chaco was known only along the banks of the Paraguay and Pilcomayo rivers, and Fiebrig (1933) was honest enough to admit that up to that time scientific exploration extended only for 100 to 150 km west of the river Paraguay (though the present author still believes that is an over-estimate)[2]. Geographically speaking the term Chaco will continue as the denomination of the whole of the region, but

[2] The first botanical collector to cross the Paraguayan Chaco by land was Teodoro Rojas, who followed the Paraguayan lines during the 'Chaco War' and reached the Parapetí river in Bolivia in 1935. More evidence comes from the zoological field; the endemic peccary genus *Catagonus*, considered for long as extinct and known only from fossils, was rediscovered as late as in 1972 in the heart of the Paraguayan Chaco (Wetzel et al., 1975).

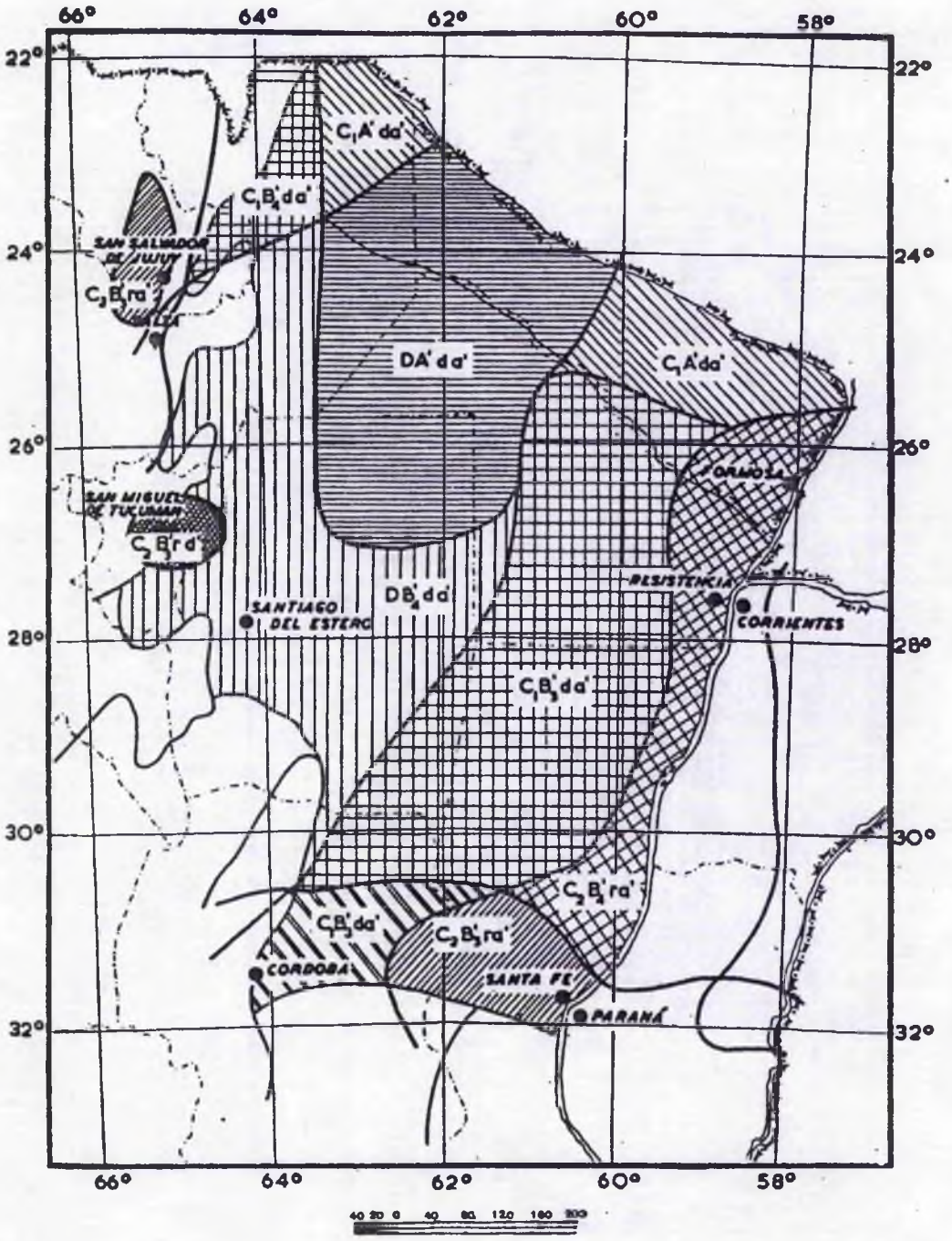


Fig. 8.1: Climate types for the Argentine Chaco, according to the 2nd system of Thornthwaite. Modified from Galmarini & Raffo del Campo, 1964.

from a phytogeographical point of view the name must have a more restricted usage.

There are no comprehensive surveys or descriptions of the Bolivian Chaco. Only Herzog's travel notes (1910, 1912), and brief comments in Cárdenas (1945), Braun (1956), Coro (1956), Unzueta (1975), Werding (1976), and Velásquez et al. (1988) are available. Herzog (op. cit.) found west of Puerto Suárez up to the Santiago Sierras communities resembling those of Prado et al. (in press b) surveyed in Mato Grosso do Sul, and he correctly regarded them as related to the Pantanal vegetation and the Caatingas rather than to the Chaco. No true Chaco vegetation is described in his notes until, when travelling from the Sierras of Chiquitos to the Río Grande, he found a low xerophilous formation, rich in spiny shrubs and cacti, known as 'Monte' and comprising *Aspidosperma quebracho-blanco* , *Caesalpinia paraguariensis* , *Capparis* spp., *Maytenus vitis-idaea* , *Bulnesia sarmientoi* , etc.. The description of Chaco vegetation in Unzueta (1975, pp 209-218, *sub* 'Bosque Seco Templado') is very shallow, and the mixed floristic list indicates that no distinction was made between the true Chaco and the non-chaquenian neighbouring formations (such as the 'Palo blanco' forest), differences that have been pointed out by previous authors (Herzog, 1910 & 1912; Coro, 1956) in their skilful, albeit brief, surveys.

However, to what extent the Chaco vegetation expands to the north of the line Chiquitos-Santa Cruz de la Sierra remains to be seen. Herzog (1912) hypothesized that the 'monte' would not go beyond 16º LS, whereas Ellenberg's (1981) map of the Bolivian ecoregions presents the Chaco (*sub* 'monte semiárido bajo') extending north through the Rio Grande plains only up to 17º LS. What is certain is that the Chaco does not reach the Llanos de Mojos in NE Bolivia (approx. 12º LS to 15º LS), as implied by Cabrera & Willink's (1980) map. The Llanos de Mojos have been studied in part by Beck (1984), Haase & Beck (1989), and Haase (1989 & 1990), and some communities show strong links with the savannas of N. South America, while the 'chaparral' resembles the Humaitá savannas and the Cerrados of central Brazil (Haase & Beck, 1989). Although the vegetation of this area comprises some very few and isolated Chaco elements (Beck, 1984), it is far from being chaquenian in character.

Most of the works on the Paraguayan Chaco (Hochreutiner, 1923; Fiebrig, 1933; Rojas & Carabia, 1945; Tortorelli, 1967) have been very shallow. More recent works have improved the state of the knowledge of the area. Esser's contributions (1982 & 1984) although focused mainly in cacti vegetation have provided a very interesting classification of the Paraguayan Chaco formation and the most detailed vegetation map available (Esser, 1982). It is noteworthy that this last author has characterized the vegetation of the eastern Paraguayan Chaco as transitional ('Übergangsgebiet') since in this area the hygrophilous elements find their westernmost limit (Esser, 1982 & 1984), which is in agreement with the views of the present author.

More recently, during the course of this study, a general survey of the Paraguayan Chaco was published by Ramella & Spichiger (1989; see also Spichiger & Ramella, 1989). Their data on the gallery forests along the river Paraguay tributaries in SE Paraguayan Chaco and those along the Timane-Lagerenza river in the northwest of the region show a floristic composition which unmistakably excludes them from the Chaco *s.s.*. They are dominated by relatively hygrophilous species such as *Calycophyllum multiflorum* , *Pisonia zapallo* , *Maclura tinctoria* , *Albizia polyantha* , *Geoffroea striata* (Spichiger & Ramella, 1989; Ramella & Spichiger, 1989), which clearly link these forests to communities **A**, **B**, **D** and **E** in Table 6.1 and separated here from the Chaco *s.s.*. The descriptions, diagrams and remarks of Ramella & Spichiger (1989) on the vegetation of the scattered hills of NW Paraguayan Chaco are of extreme interest. While surrounded by true Chaco vegetation on the plains, the slopes of the Cerro León and Cerro Cabrera are covered by a deciduous forest of *Anadenanthera colubrina* (very probably var. *cebil*), accompanied by *Pterogyne nitens* , *Astronium urundeuva* , *Amburana cearensis* and *Aspidosperma pyrifolium* , which not only show a very strong link with the 'Palo blanco' forest in NW Argentina and the calcareous forests around Corumbá, but also an amazing resemblance of the arboreal caatinga vegetation of NE Brazil (cf. Ch. 3). On top of these hills cerrado-like vegetation has been found, that is savannas of *Tabebuia caraiba* , *Jacaranda cuspidifolia* and *Pseudobombax campestre* (Ramella & Spichiger, 1989). This sequence of

vegetation seems to be repeated in the Santiago and Chiquitos Sierras of Bolivia (Herzog, 1910 & 1912).

By excluding these extraneous communities it is now possible to re-establish the geographical limits of the Chaco as a phytogeographical province. On the basis of a strict floristic list of woody and succulent species (Sect. 4.1), phytosociological study of the more relevant plant communities in the region both in classical and numerical analyses (Ch. 6), and putting the vegetation of this area against the background of similar formations in South America, a map of what is here regarded as Chaco *s.s.* is presented (Fig. 8.2). It must be noted that the Sierra Chaco, although taken as a separate entity throughout the analysis in Ch. 6, is accepted as part of the Chaco *s.s.*; however, the *Polylepis australis* woodlands occurring in the Córdoba Sierras should not be regarded as chaquenian, as in Cabrera (1976). These communities comprise basically an Andean flora with little contact with the Chaco itself (Vuilleumier, 1986; Cabido, *in litt.*), and their restriction to N Argentina appear to be attributable to range retraction of the progenitor of *P. australis* during Pleistocene events (Simpson, 1986). In the construction of this new map some previous vegetation maps have been employed; i.e. Coro (1956) and Ellenberg (1981) for the Bolivian Chaco, Vervoorst (in Hawkes & Hjerting, 1969) for NW Argentina up to La Rioja province, Ragonese & Castiglioni (1970) for SW Chaco in the provinces of La Rioja, San Juan, San Luis and Córdoba in part, Sayago (1969) and Luti et al. (1979) for the Córdoba province, and Lewis (1981) for the southern and eastern limit in the Santa Fe province. Also taken into consideration were the maps of the neighbouring phytogeographic provinces Monte (Morello, 1958) and Espinal (Lewis & Collantes, 1973). The extremely patterned vegetation in the east of the Chaco *s.s.* cannot be mapped with any precision at this stage with the knowledge available to date. A wide belt of transitional vegetation has been left open to further studies which could determine the exact localities where true Chaco vegetation can be found. However, to delimit this belt, information was taken from maps in Castellanos & Pérez-Moreau (1944), Morello & Adámoli (1967), Ragonese & Castiglioni (1970), Lewis (1981), Esser (1982), and Prado et al. (in press b), together with the present author's field experience and the plant distribution maps here presented (Ch. 5).

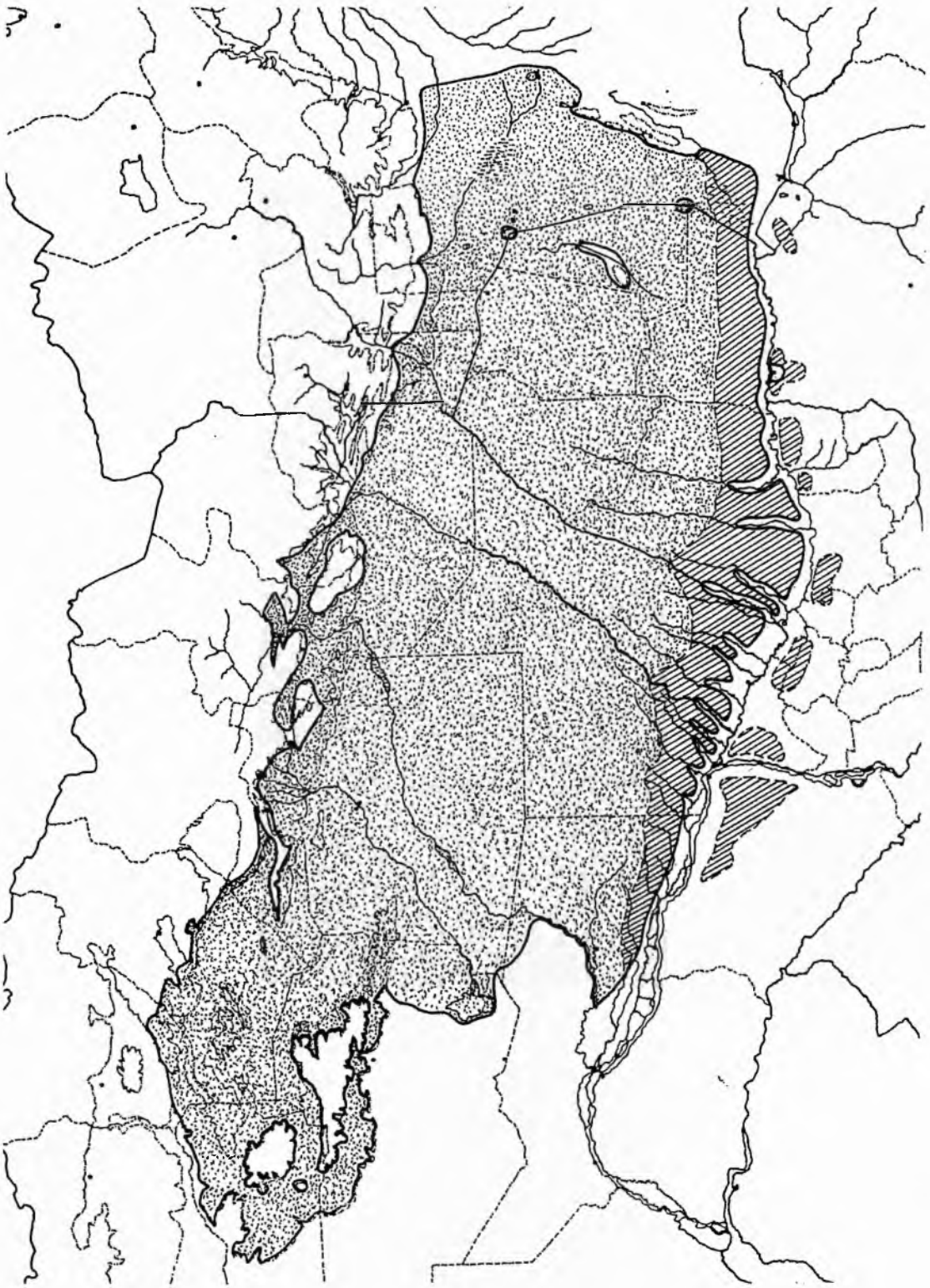


Fig. 8.2: A new proposal for the geographical limits of the Chaco *s.s.*. The transitional belt is indicated by oblique hatching.

8.2- Chaco *versus* Caatingas:

The idea that there exist strong links between the flora of the Caatingas and Chaco provinces owes much to Dárdano de Andrade-Lima, and the views he expressed in his analysis of the origins of the caatinga flora. Andrade-Lima firmly believed that the flora of the Caatingas was "largely of alien origin, especially at the generic level, and to a lesser degree at the species level", and that these elements "appear have reached the area by a SW-NE migratory route", such that "the source of the majority of caatinga taxa appears to have been the northern part of the Argentinian-Paraguaian-Bolivian Chaco" (Andrade-Lima, 1982, p. 247).

In this latter work Andrade-Lima listed some tree species which, according to him, are subxerophytic or xerophytic plants which are common in arid areas elsewhere but possess disjunctions in NE Brazil. Such examples for the Chaco-Caatingas disjunction were: *Schinopsis brasiliensis* , both the typical and the *glabra* varietes, *Anadenanthera colubrina* var. *cebil* (sub *A. macrocarpa*), *Amburana cearensis* , *Pterogyne nitens* , *Phytolacca dioica* , and *Prosopis ruscifolia* . In fact, however, except *P. ruscifolia* none of these last species are found in any typical Chaco *s.s.* forest community, but only in river valley vegetation in the eastern border of the Chaco (rivers Paraná, Paraguay, and tributaries), and in the 'Palo blanco' and 'Tipa-Pacará' forests to the west of the Chaco (see Sect. 8.1). This is particularly the case of *Anadenanthera colubrina* var. *cebil* (Altschul, 1964, and Fig. 5.38), *Amburana cearensis* and *Pterogyne nitens* (Fig. 5.40 & 5.43), which are sometimes members of gallery forests in Western Chaco in Argentina but are regarded as non-chaquenian species (Morello & Saravia Toledo, 1959a & b; Adámoli et al., 1972). *Schinopsis brasiliensis* is not a Chaco species in any sense, but rather it is a common tree in NE Brazil in arboreal caatinga (Andrade-Lima, 1981), and its distribution extends towards south, interrupted by cerrado formations, to reappear in Mato Grosso do Sul and northern Paraguay in the vicinity of the river Paraguay, and in Bolivia along the Santiago and Chiquitos ranges and the Yungas area (see Fig. 5.46). Likewise, the Argentine 'ombú', *Phytolacca dioica* , is not a true Chaco species but rather a common tree in the tall forests bordering the river Paraná valley with very few

intrusions of chaquenian character (see Fig. 5.81; also Klein, 1972, and Prado et al., in press a).

The case of *Prosopis ruscifolia* merits a separate analysis; it is in fact a Chaco endemic, since its dispersion area is fully located inside the Chaco *s.s.* (Fig. 5.7), whereas its presence in the Monte province as stated by Andrade-Lima (1982) has never been established. What is extremely doubtful, however, is whether this species occurs in the Caatingas. All known exsiccata come from a single very old tree in the vicinity of Cachoeira do Roberto, Pernambuco (Neiva & Pena, 1916; Luetzelburg, 1922-23; Ducke, 1953; Andrade-Lima, 1954; Bigarella et al., 1975), which was "once a prosperous village on the cattle trail from Bahia to Piauí" (Andrade-Lima, 1954, p.57). Burkart monographed the genus and confirmed the identity of this specimen but he wondered if this single tree could be a casual introduction to the area (Burkart, 1976, p.248). However, Andrade-Lima (1954 & 1982) took this isolated individual as proof of Chaco species migration to NE Brazil in a drier climatic phase, assuming that other individuals have probably disappeared through the progressive erosion of the area. But *Prosopis ruscifolia* trees live only a moderate life-span, reaching occasionally 80 years (Morello et al., 1971), and it is a very aggressive woody weed in its natural area in Argentina, with a highly palatable indehiscent pod for large herbivores and very particularly for cattle, and so with seeds suited to endozoochorous dispersion (Morello et al., 1971; Burkart, 1976). These characteristics make this species a successful colonizer of disturbed environments in the Chaco. Moreover, the location of this individual in the Caatingas is separated by more than 2,300 km from the bulk of the species in the Chaco, and there is not a single collection or reference to its presence in the intervening area, contrary to what has been shown in Ch. 5 for numerous other species which do link the Caatingas to other seasonal formations of South America. Thus, the evidence points to its occurrence as a casual introduction to NE Brazil, probably through imported cattle.

The levels of generic and specific endemicity given for Chaco and Caatingas in Ch. 5 are in agreement with the Takhtajan (1986) criteria employed to characterize floristic provinces of the world, and the higher figures for the Brazilian area seem to follow an expected

latitudinal increment of endemisms (see Major, 1988): tropical Caatingas, as opposed to temperate/subtropical Chaco. Moreover, the Caatingas are far richer than the monotonous Chaco plains in providing varied and numerous habitats (cf. Ch. 3 & 2). Both provinces are then very well defined from this point of view, and even allowing for an overestimation of the degree of endemicity, when compared to Major's table (1988) for several regions of the world they are equivalent to those e.g. of the Sonoran desert and the Sahara as regards the Chaco, and to the California floristic province and the Canary islands for the Caatingas. There is no reason, therefore, to regard the Caatingas flora as too low in endemics, as repeatedly stated by Rizzini (1963 & 1979), and more emphatically by Andrade-Lima (1982), who even suggested that the area could not have its own unique flora. On the contrary, the percentages of autochtonous and alien genera and species in the Caatingas are in all probability as high as those of any other well defined floristic province of the world, and even comparable to those of certain islands which usually concentrate the highest figures of endemicity (Major, 1988).

In the Introduction of this thesis it has been mentioned that most of the alleged botanical links between Chaco and Caatingas are usually described as pairs of vicariant species (Rizzini, 1963; Veloso, 1964). The currently generally accepted concept of vicariance states that "if populations occupying separate areas are clearly descended from an immediate common ancestor, but are distinct enough in external morphology so that the systematist can always tell them apart, they are known as vicarious species" (Stebbins, 1950). Thus, a detailed knowledge of systematic relationships within the genus is a prerequisite to establish vicariant status with a reasonable degree of certainty. Some of the genera involved in the Chaco-Caatingas links have never been studied monographically since Martius' Flora Brasiliensis, e.g. *Ziziphus* , *Caesalpinia* , *Capparis* . Other genera have had formal taxonomic revisions, e.g. *Schinopsis* (Meyer & Barkley, 1973), *Astronium* (Barkley, 1968), and *Copernicia* (Dahlgren & Glassman, 1961), but with no emphasis on species relationships presented by these authors. However, some preliminary comments and conclusions can be made in these cases.

The genus *Schinopsis* consists of eight species, seven of which were accepted by Meyer & Barkley (1973), and the eighth is the recently reinstated *S. heterophylla* (Muñoz, 1990), apparently a hybrid between *S. quebracho-colorado* and *S. balansae* . However, the present author believes that *S. heterophylla* is conspecific with *S. cornuta* , another species recognized by Meyer & Barkley (1973) and which is the earlier binomial of the two available. With regard to the other species, the characters employed to separate the poorly collected *S. peruviana* from *S. brasiliensis* , that is to say smaller, more numerous leaflets for the former, can be found on the juvenile shoots of the latter. It is presumed likely, therefore, that *S. peruviana* is in fact conspecific with *S. brasiliensis* . Moreover, it is considered that another species, *S. glabra* , likewise does not merit specific status and should be kept as a variety of *S. brasiliensis* , as originally described by Engler. Thus, the genus would be reduced to only five species: *S. brasiliensis* , endemic to the Pleistocenic Arc; *S. quebracho-colorado* and *S. cornuta* , two Chaco endemics; the unifoliolate *S. balansae* ; and the orophilous *S. haenkeana,* characteristic of the Sierra Chaco but sometimes present in the 'palo blanco' Forest. If vicariant taxa occur in this genus, it is considered that the most likely case is the pair *S. brasiliensis -S. haenkeana* , which are morphologically very close. Vicariance between *S. brasiliensis* and *S. quebracho-colorado* cannot be ruled out, but they show rather more strongly delimited morphological differences (see Prado et al., in press b) than the previous pair of species.

In the genus *Astronium* , the most obviously closest species to the Caatingas tree *Astronium urundeuva* is *A. balansae* [3], clearly distributed along the Paraguay-Paraná river system (Fig. 5.83) and not in the Chaco s.s. (although a number of researchers would argue it is a true Chaco species). The case of the genus *Copernicia* also allows for some preliminary conclusions, based on the infrageneric arrangement by Dahlgren & Glassman (1961). There are only three species in South America, which are regarded as relatively recent immigrants (Uhl & Dransfield, 1987, pp 204-5): *C. tectorum* (=*C. sancta-martae*) in the Venezuelan Llanos and dry Caribbean vegetation; *C. cerifera* (=*C.*

[3] Recently Santin (1991) has separated these two species in the reinstated genus *Myracrodruon* .

prunifera) exclusive to the Caatingas; and *C. alba* (=*C. australis*) in the Brazilian Pantanal, E Bolivia, central Paraguay along the river Paraguay, and NE Argentina extending well inside the Chaco *s.s.*. The rest of the genus is mainly confined to the center of distribution in the Greater Antilles, with more than 20 species in Cuba, and two in neighbouring Hispaniola. Both *C. tectorum* and *C. cerifera* have been placed in the Subgenus *Copernicia* , but *C. alba* is on its own in the Subgenus *Coperniciopsis* . The most plausible vicariant pair, therefore, is likely to be a Caribbean-NE Brazil species link, and not *C. cerifera* -*C. alba* as claimed by Rizzini (1963).

The genus *Aspidosperma* , recently studied by Marcondes-Ferreira (1988) and widespread in every subtropical and tropical woody community from Mexico to Argentina (except Chile), consists of 33 species grouped in two subgenera, one with 9 sections and comprising 31 species. The Caatingas species are mainly placed in two sections; sect. *Polyneura* , considered to be relatively unspecialized within the genus, contains *A. polyneuron* and *A. cuspa* , the latter regarded as ancestral species by Marcondes-Ferreira (1988); and sect. *Aspidosperma* , where *A. pyrifolium* (by far the most important *Aspidosperma* in the Caatingas) is located together with the widespread cerrado species *A. tomentosa* and *A. macrocarpum* . On the other hand, the two very close chaquenian species *A. quebracho-blanco* and *A. triternatum* are isolated in the most evolved and southernmost sect. *Pungentia* , which is very easily distinguished from the rest of the genus. If this infra-generic scheme is correct, it is unlikely that any vicariad-type links exist between the caatinga and chaquenian species of *Aspidosperma* , as alleged by Rizzini (1963) and Veloso (1964).

A different case is posed by the genus *Geoffroea* ; if the present author's criterion is accepted, i.e. regarding *G. striata* and *G. spinosa* as a polymorphic unit and very probably a single species, *Geoffroea* would be reduced to only two species which are certainly vicariads: *G. decorticans* in the Chaco and some related provinces (see Fig. 5.16), and *G. striata/spinosa* in Caatingas, W Ecuador, N Venezuela, central Bolivia and the Paraguay-Paraná system (Fig. 5.58). This would constitute the only unmistakable example of vicariance involving Chaco

and Caatingas at species level, but it should be noted that neither of the two are exclusive to their provinces.

It can be concluded that vicariance links between Chaco and Caatingas are very weak if they exist at all, and that Andrade-Lima's (1982) proposed migratory route SW-NE, in so far it refers to the Chaco flora has to be rejected altogether. There is no chaquenian floristic element following that route up to the Caatingas, and as noted above all of Andrade-Lima's examples are flawed. On the contrary, in some cases the route seems to be exactly the opposite, as the genera *Copernicia* and *Aspidosperma* suggest. We can thus safely reject the proposal that a strong component of the Caatingas flora derives from the Chaco province (Andrade-Lima, 1982), and likewise Rizzini's (1963 & 1979) statement that the Caatingas elements have their origin in equal proportions from the Chaco and the Atlantic rainforest.

There are in fact only three woody species in common between Chaco and Caatingas (Table 8.1): *Parkinsonia aculeata* , *Ximenia americana* , and *Sideroxylon obtusifolium* . Their presence in both areas, however, is meaningless in this context since all three species have very widespread distributions from Mexico to Argentina, occurring in numerous vegetation types, whilst *Ximenia americana* is even pantropical. Besides, the floristic links of the Chaco should be looked for in another direction. Sarmiento (1972 & 1975) showed that the relationship Monte-Chaco is stronger than any other link Monte-arid and semiarid areas in South America, and furthermore, the floristic contacts of the Chaco with dry Andean valleys and the Sonora desert must not be overlooked.

Rather, the floristic dissimilarities between the Chaco and Caatingas are striking, and these most likely lie in the lack of common physical environmental features between these two areas. Thus, there is a fundamental difference in their geological origin and geomorphology: the Chaco comprises huge sedimentary, monotonous plains of both æolian and more recent alluvial genesis, modelled by a basically endorheic river system. In contrast, the Caatingas are undulating peneplains of erosive origin which left the ancient Pre-Cambrian Brazilian shield exposed and furrowed by numerous short-lived exorheic

TABLE 8.1: **Genera and species in common between Chaco *s.s.* and Caatingas.**

GENERA	SPECIES	References for Chaco
1- *Acacia*		Cialdella, 1984
2- *Aspidosperma*		Marcondes-Ferreira,1988
3- *Ayenia*		Cristóbal, 1960
4- *Bauhinia*		Fortunato, 1986
5- *Bougainvillea*		Toursarkissian, 1975
6- *Bromelia*		Smith & Downs, 1974-79
7- *Caesalpinia*		Burkart, 1952
8- *Capparis*		Gómez, 1953
9- *Ceiba*		Gibbs (pers. comm.)
10- *Celtis*		Morello & Adámoli, 1974
11- *Cereus*		Kiesling, 1975
12- *Copernicia*		Morello & Adámoli, 1974
13- *Coursetia*		Lavin, 1988
14- *Croton*		Sayago, 1969
15- *Desmanthus*		Burkart, 1952
16- *Dyckia*		Smith & Downs, 1974-79
17- *Eriocereus*		Kiesling, 1975
18- *Erythroxylum*		Morello et al., 1971
19- *Euphorbia*		Subils, 1977
20- *Geoffroea*		Burkart, 1952
21- *Ipomoea*		Sayago, 1969
22- *Jacaratia*		Badillo, 1971
23- *Jatropha*		Castellanos, 1958
24- *Lippia*		Luti et al., 1979
25- *Maytenus*		Morello & Adámoli, 1974
26- *Mimosa*		Burkart, 1952
27- *Opuntia*		Kiesling, 1975

28- *Parkinsonia*	*aculeata* L.	Burkart, 1952
29- *Pavonia*		Sayago, 1969
30- *Pereskia*		Leuenberger, 1986
31- *Quiabentia*		Castellanos, 1952
32- *Ruprechtia*		Cocucci, 1958
33- *Sapium*		Jablonski, 1967
34- *Schinopsis*		Meyer & Barkley, 1973
35- *Senna*		Irwin & Barneby, 1982
36- *Sida*		Sayago, 1969
37- *Sideroxylon*	*obtusifolium* (Roem. & Schult.) Pennington **subsp.** *obtusifolium*	Pennington, 1990
38- *Solanum*		Morton, 1976
39- *Tabebuia*		Morello & Adámoli, 1974
40- *Wissadula*		Morello & Adámoli, 1974
41- *Ximenia*	*americana* L.	Sleumer, 1984
42- *Ziziphus*		Morello & Adámoli, 1974

streams. There are also important differences in climate between the two areas: no area within the Chaco *s.s.* is free from frosts, and although the mean annual temperature is relatively low (17 to 24ºC, from south to north), most of the area is enclosed within the highest absolute maxima isotherm of South America (47ºC), and there is a moderate variation coefficient of yearly rainfall (from 0.2 to 0.3, in Galmarini & Raffo del Campo, 1964). In contrast, the occurrence of frosts in the tropical Caatingas has never been registered, and whilst the mean annual temperature is higher (26 to 28ºC), the absolute maxima is rarely over 40ºC. There is an extreme rainfall irregularity with the variation coefficient up to 0.55 and periodical catastrophic droughts lasting over a year long. With regard to soils, the main features of the Chaco *s.s.* are particles smaller than 2 mm, generalized poor drainage because of clay textured horizons, abundance of salts and high pH. The Caatingas soils, on the other hand, are characteristic for the abundance of pebbles, stones and massive rock outcroppings, scarcity of saline areas because of the good drainage and the exorheic river system, and pH probably tending to neutral.

There is an additional and interesting ecological-floristic difference between Chaco and Caatingas. The river valleys vegetation and gallery forests in NE Brazil comprise some widespread species (*Erythrina velutina* , *G. striata/spinosa* , *Sideroxylon obtusifolium*), endemic elements of the Caatingas (*Ziziphus joazeiro* , *Maytenus rigida* , *Capparis yco* , *Pilosocereus gounellei* , *Cereus jamacaru*), and even two species which are not only endemic but can be found solely in these environments: *Copernicia cerifera* and *Licania rigida* . On the contrary, the homologous vegetation in the Chaco plains is generally dominated by alien elements of widespread tropical distribution (including extensions to the Caatingas!), or species which grow in nearly pure populations in riverine conditions all over the continent (*Salix humboldtiana* , *Tessaria integrifolia*). There is certainly no endemic chaquenian species restricted to riparian environments, as found in the Caatingas. This may reflect a relative lack of isolation, or indicate that present climatic conditions in the Caatingas, and consequently the hydrographic regime, have prevailed for a longer period than those of the Chaco, where there was not enough evolutionary time for speciation of

Chaco taxa but rather a more recent invasion of alien elements better adapted to such habitats.

At the beginning of this study two basic methodological approaches were adopted: (a) to build up reliable data base of floristic lists of the major phytogeographical units involved, and (b) to map accurately the distributions of the more important woody species involved in the Chaco and Caatingas regions. It soon became apparent that the Caatingas species, far from appearing in the Chaco, were conspicuous by their absence from this area, although many taxa occurred in formations peripheral to the Chaco *s.s.*. From the comparison of the Chaco and Caatingas floristic lists (Sect. 4.1 & 4.2) arouse Table 8.1 shown above, recording all genera and the only three woody species they have in common. The same comparison was made for the Caatingas and the Subandean Piedmont Forests floristic lists; the results are shown in Table 8.2. There are 51 woody and succulent species and 109 genera in common between the Caatingas and the 'Palo blanco' and 'Tipa-Pacará' deciduous forests.

A similar comparison was performed with what was called here '2nd nucleus' of the Pleistocenic Arc (see Sect. 5.3.1), that is to say the area encompassed by the Paraguay-Paraná river system in central Paraguay and NE Argentina. This area groups a number of different but related formations of which a floristic list is not here provided, and consists of a rather arbitrary clustering of plant communities that can be provisionally equated to Cabrera & Willink's (1980) 'Selva Subtropical Paranense' in the Paranense phytogeographic province. However, the presence or absence of Caatingas elements was anyhow confirmed through the relevant literature, as cited in Table 8.3, and they share 66 species and 109 genera.

In Table 8.4 the results of the floristic comparison is summarized; the percentages of the total flora of the Caatingas represented by the number of species and genera in common is provided. Thus, it can be seen that only 0.69% of the woody and succulent species of the Caatingas are recorded for the Chaco *s.s.*, and 21.11% of all Caatingas genera. More striking figures are obtained derived from the comparison of the Caatingas flora with the '2nd nucleus' and '3rd

TABLE 8.2: **Genera and species in common between the Subandean Piedmont Forests and Caatingas.**

GENERA	SPECIES	References for Sub-Andean Piedmont Forests
1- *Acacia*		Cialdella, 1984
2- *Aechmea*		Ragonese & Castigl., 1970
3- *Aeschynomene*		Burkart, 1952
4- *Albizia*	*polyantha* (Spr. f.) Lewis	Adámoli et al., 1972
5- *Amburana*	*cearensis* (Fr.All.) Smith	Cabrera, 1976
6- *Anadenanthera*	*colubrina* (Vell.) Bren. **var.** *cebil* (Grisebach) Altschul	Cabrera, 1976
7- *Arrabidea*	*corallina* (Jacq.) Sandw.	Fabris, 1965
8- *Aspidosperma*	[Bolivia]	Marcondes-Ferreira,1988
9- *Astronium*	*urundeuva* (Fr.All.) En.	Cabrera, 1976
10- *Ayenia*	*tomentosa* L. [Bolivia]	Cristóbal, 1960
11- *Bauhinia*		Fortunato, 1986
12- *Bougainvillea*		Toursarkissian, 1975
13- *Brasiliopuntia*		Castellanos, 1944
14- *Bromelia*		Smith & Downs, 1974-79
15- *Brunfelsia*	*uniflora* (Pohl) D.Don	Plowman, 1979
16- *Byttneria*	*scabra* L. [Bolivia]	Cristóbal, 1976
17- *Caesalpinia*		Burkart, 1952
18- *Calliandra*		Burkart, 1952
19- *Canavalia*	*brasiliensis* Mart. ex Benth.	Burkart, 1952
20- *Capparis*		Meyer, 1944

21- *Carica*	*quercifolia* (St.-Hil.) Hier.	Badillo, 1971
22- *Ceiba*		Gibbs (pers. comm.)
23- *Celtis*	*pubescens* (Kth.) Spreng.	Romanczuk &Mart., 1978
24- *Cereus*		Adámoli et al., 1972
25- *Chamaecrista*		Irwin & Barneby, 1982
26- *Cnidoscolus*	*vitifolius* Mill. ex Pohl	Legname, 1982
27- *Cochlospermum*	*vitifolium* (W.) Spr.[Bol.]	Poppendieck, 1981
28- *Combretum*	*leprosum* Mart.[Bolivia]	Exell, 1953
29- *Copaifera*	[Bolivia]	Dwyer, 1951
30- *Copernicia*		Dahlgren & Glass., 1961
31- *Cordia*	*trichotoma* (Vell.) Arrab. ex Steud.	Legname, 1982
32- *Coursetia*		Lavin, 1988
33- *Coutarea*	*hexandra* (Jacq.)Schum.	Legname, 1982
34- *Croton*		Legname, 1982
35- *Dasyphyllum*		Cabrera, 1953
36- *Desmanthus*	*virgatus* (L.) Willd.	Burkart, 1952
37- *Ditaxis*		O'Donell & Lourteig, 1942
38- *Dyckia*		Smith & Downs, 1974-79
39- *Enterolobium*	*contortisiliquum* (Vell.) Morong	Cabrera, 1976
40- *Eriotheca*		Robyns, 1963
41- *Erythrina*		Cabrera, 1976
42- *Erythroxylum*		Legname, 1982
43- *Espostoa*	[Bolivia]	Buxbaum, 1959 & 1969
44- *Euphorbia*		Subils, 1977
45- *Galphimia*	*brasiliensis* (L.) A.Juss. [Bolivia]	Niedenzu, 1928

46- *Geoffroea*	*striata* (W.)Morong [Bol.]	herbarium specimens
47- *Heteropterys*	*syringifolia* Griseb.[Bol.]	Niedenzu, 1928
48- *Ipomoea*	*carnea* Jacq. **subsp.** *fistulosa* (Mart. ex Ch.) D. Austin	O'Donell, 1959
49- *Jacaranda*		Digilio & Legname, 1966
50- *Jacaratia*		Badillo, 1971
51- *Jatropha*		Pax, 1959
52- *Lagascea*	*mollis* Cav.	Stuessy, 1978
53- *Lantana*		Devoto & Rothkugel, 1942
54- *Lippia*		Devoto & Rothkugel, 1942
55- *Lonchocarpus*		Legname, 1982
56- *Loxopterigium*		Legname, 1982
57- *Luehea*		Legname, 1982
58- *Machaerium*	*acutifolium* Vog.	Burkart, 1952
59- *Maclura*	*tinctoria* (L.)Don ex Steud	Vázquez Ávila, 1985
60- *Manihot*		Rogers & Appan, 1973
61- *Maytenus*		Legname, 1982
62- *Melochia*		Goldberg, 1967
63- *Mimosa*		Burkart, 1952
64- *Myroxylon*	*balsamum* (L.) Harms	Cabrera, 1976
65- *Opuntia*		Kiesling, 1975
66- *Parapiptadenia*		Cabrera, 1976
67- *Patagonula*		Legname, 1982
68- *Pavonia*		Meyer, 1963
69- *Peltophorum*	*dubium* (Spr.)Taub. [Bol.]	herbarium specimens
70- *Pentapanax*		Meyer, 1944
71- *Pereskia*		Leuenberger, 1986
72- *Petiveria*	*alliacea* L.	Meyer, 1944
73- *Phyllostylon*		Cabrera, 1976

74- *Phytolacca*		Meyer, 1963
75- *Piptadenia*	*viridiflora* (Kth.) Benth.	Burkart, 1952
76- *Pisonia*		Meyer, 1963
77- *Pithecellobium*		Hoc, 1981
78- *Platypodium*	*elegans* Vog. [Bolivia]	herbarium specimens
79- *Pouteria*	*gardneriana* (DC.)Radlk. [Bolivia]	Pennington, unp.ms.
80- *Prockia*	*crucis* P.Browne ex L.	Cabrera, 1976
81- *Pseudobombax*		Robyns, 1963
82- *Pterocarpus*	*violaceus* Vog. [Bolivia]	Rojo, 1972
83- *Pterogyne*	*nitens* Tul.	Cabrera, 1976
84- *Ptilochaeta*		Niedenzu, 1928
85- *Quiabentia*	*zehntneri* (Br.& Rose) Br. & Rose [Bolivia]	Castellanos, 1952
86- *Randia*	*armata* (Sw.) DC.	Legname, 1982
87- *Rauvolfia*		Legname, 1982
88- *Ruprechtia*	*laxiflora* Meissn.	Cabrera, 1976
89- *Sapindus*	*saponaria* L.	Legname, 1982
90- *Sapium*		Jablonski, 1967
91- *Schinopsis*	*brasiliensis* Engler [Bol.]	Meyer & Barkley, 1973
92- *Schoepfia*		Sleumer, 1984
93- *Sebastiania*		Digilio & Legname, 1966
94- *Seguieria*	*aculeata* Jacq.	Rohwer, 1982
95- *Senna*	*spectabilis* (DC.)Ir.& Bar.	Irwin & Barneby, 1982
96- *Serjania*	*glabrata* Kunth	Radlkofer, 1956
97- *Sesbania*	*exasperata* Kunth	Burkart, 1952
98- *Sida*	*cordifolia* L.	herbarium specimens
99- *Sideroxylon*	*obtusifolium* (Roem. & Schult.) Pennington **subsp.** *obtusifolium*	Pennington, 1990
100- *Solanum*	*granuloso-leprosum* Dunal	Legname, 1982

101- *Sterculia*	*striata* S - H . & Naud.[Bol.]	herbarium specimens
102- *Stigma phyllum*	[Bolivia]	Niedenzu, 1928
103- *Swartzia*	[Bolivia]	Cowan, 1968
104- *Tabebuia*	*caraiba* (Mart.) Bur.[Bol.]	herbarium specimens
Tabebuia	*impetiginosa* (Mart. ex DC.) Standley	Gentry, 1979
105- *Terminalia*		Exell, 1940
106- *Tournefortia*	*rubicunda* Salzm. ex DC.	Devoto & Rothkugel, 1942
107- *Trichilia*		Pennington, 1981
108- *Ximenia*	*americana* L. **var.** *argentinensis* De Filipps	Sleumer, 1984
109- *Ziziphus*		Escalante, 1946

TABLE 8.3: **Genera and species in common between the vegetation of the Paraguay-Paraná river system and the Caatingas.**

GENERA	SPECIES	References for the Paraguay-Paraná river syst. vegetation
1- *Acacia*	*farnesiana* (L.) Willd.	Cialdella, 1984
Acacia	*martii* Benth.	Cialdella, 1984
Acacia	*monacantha* Willd.	Cialdella, 1984
Acacia	*polyphylla* DC.	Cialdella, 1984
2- *Acosmium*		Burkart, 1952
3- *Aechmea*		Ragonese & Castigl., 1970
4- *Aeschynomene*		Burkart, 1952
5- *Albizia*	*polyantha* (Spr. f.) Lewis	Burkart, 1952
6- *Amburana*	*cearensis* (Fr.All.) Smith	Burkart, 1952
7- *Anadenanthera*	*colubrina* (Vell.) Bren. **var.** *cebil* (Grisebach) Altschul	Cabrera, 1976
8- *Arrabidea*	*corallina* (Jacq.) Sandw.	Fabris, 1965
9- *Aspidosperma*	*cuspa* (Kunth) Blake	Marcondes-Ferreira,1988
Aspidosperma	*polyneuron* Müll. Arg.	Marcondes-Ferreira,1988
Aspidosperma	*pyrifolium* Mart.	Marcondes-Ferreira,1988
10- *Astronium*	*urundeuva* . (Fr.All.) En.	Barkley, 1968
11- *Ayenia*	*tomentosa* L. [Bolivia]	Cristóbal, 1960
12- *Balfourodendron*	*riedelianum* (Engl.)Engl.	Cabrera, 1976
13- *Bauhinia*	*forficata* Link	Fortunato, 1986
14- *Brasiliopuntia*		Castellanos, 1944

15- *Bromelia*		Smith & Downs, 1974-79
16- *Brunfelsia*		Plowman, 1979
17- *Byttneria*	*scabra* L.	Cristóbal, 1976
18- *Caesalpinia*		Burkart, 1952
19- *Calliandra*		Burkart, 1952
20- *Calopogonium*		Burkart, 1952
21- *Campomanesia*		Landrum, 1986
22- *Canavalia*		Burkart, 1952
23- *Capparis*		Gómez, 1953
24- *Carica*	*quercifolia* (St.-Hil.) Hier.	Badillo, 1971
25- *Ceiba*		Gibbs (pers. comm.)
26- *Celtis*	*pubescens* (Kth.) Spreng.	Romanczuk &Mart., 1978
27- *Cereus*		Cabrera, 1976
28- *Chamaecrista*	*desvauxii* (Coll.) Killip	Irwin & Barneby, 1982
Chamaecrista	*rotundifolia*(Pers.)Green.	herbarium specimens
29- *Cnidoscolus*		Pax, 1958
30- *Combretum*	*fruticosum* (Loefl.)Stuntz	Exell, 1953
Combretum	*lanceolatum* P.ex Eichl.	Exell, 1953
Combretum	*laxum* Jacq.	Exell, 1953
Combretum	*leprosum* Mart.	Exell, 1953
31- *Copaifera*	*langsdorffii* Desf.	Burkart, 1952
32- *Copernicia*		Dahlgren & Glass., 1961
33- *Cordia*	*trichotoma* (Vell.) Arrab. ex Steud.	Cabrera, 1976
34- *Coursetia*		Lavin, 1988
35- *Coutarea*	*hexandra* (Jacq.)Schum.	Devoto & Rothkugel, 1942
36- *Crateva*	*tapia* L.	Gómez, 1953
37- *Cratylia*		Burkart, 1952
38- *Croton*		Cabrera, 1976

39- *Dalbergia*	*frutescens* (Vell.) Britt.	Burkart, 1952
40- *Dasyphyllum*		Cabrera, 1953 & 1959
41- *Desmanthus*	*virgatus* (L.) Willd.	Burkart, 1952
42- *Dicella*	*bracteosa* (A.Juss.) Gris.	Niedenzu, 1928
43- *Dioclea*		Burkart, 1952
44- *Discolobium*		Burkart, 1952
45- *Ditaxis*		Pax & Hoffmann, 1958a
46- *Dyckia*		Smith & Downs, 1974-79
47- *Enterolobium*	*contortisiliquum* (Vell.) Morong	Burkart, 1952
48- *Erythrina*		Cabrera, 1976
49- *Erythroxylum*		Cabrera, 1976
50- *Euphorbia*		Subils, 1977
51- *Galphimia*	*brasiliensis* (L.) A.Juss.	Niedenzu, 1928
52- *Geoffroea*	*striata* (Willd.)Morong	Burkart, 1949
53- *Guettarda*		Boelcke, 1981
54- *Heteropterys*	*syringifolia* Griseb.	Niedenzu, 1928
55- *Hymenaea*	*courbaril* L. **var.** *stilbocarpa* (Hayne)Lee&Lang.	Lee & Langenheim, 1975
Hymenaea	*martiana* Hayne	Lee & Langenheim, 1975
56- *Ipomoea*	*asarifolia* (Desr.) Roem. & Schult.	O'Donell, 1959
Ipomoea	*carnea* Jacq. **subsp.** *fis-tulosa*(Mart.ex Ch.)Aust.	O'Donell, 1959
57- *Jacaratia*		Badillo, 1971
58- *Jatropha*		Pax, 1959
59- *Lagascea*	*mollis* Cav.	Stuessy, 1978
60- *Lantana*		Devoto & Rothkugel, 1942

61- *Lippia*		Devoto & Rothkugel, 1942
62- *Lonchocarpus*		Burkart, 1952
63- *Luehea*		Cabrera, 1976
64- *Machaerium*	*acutifolium* Vog.	Burkart, 1952
65- *Maclura*	*tinctoria* (L.)Don ex Steud	Vázquez Ávila, 1985
66- *Manihot*		Rogers & Appan, 1973
67- *Maytenus*		herbarium specimens
68- *Melochia*		Goldberg, 1967
69- *Mimosa*	*hexandra* Micheli	Burkart, 1952
Mimosa	*pigra* L.	Burkart, 1952
70- *Opuntia*		Kiesling, 1975
71- *Parapiptadenia*		Cabrera, 1976
72- *Patagonula*		Cabrera, 1976
73- *Pavonia*		herbarium specimens
74- *Peltophorum*	*dubium* (Spr.)Taub.	Burkart, 1952
75- *Pentapanax*		herbarium specimens
76- *Pereskia*		Leuenberger, 1986
77- *Petiveria*	*alliacea* L.	Franceschi et al., 1985
78- *Phyllostylon*		Cabrera, 1976
79- *Phytolacca*	*dioica* L.	Lewis & Pire, 1981
80- *Pisonia*		Prado et al., in press a
81- *Pithecellobium*		Hoc, 1981
82- *Platypodium*	*elegans* Vog.	herbarium specimens
83- *Poecilanthe*		Burkart, 1952
84- *Pouteria*	*gardneriana* (DC.)Radlk.	Pennington, 1990
85- *Pterocarpus*		Burkart, 1952
86- *Pterogyne*	*nitens* Tul.	Cabrera, 1976
87- *Randia*	*armata* (Sw.) DC.	Boelcke, 1981
88- *Ruprechtia*	*laxiflora* Meissn.	Cabrera, 1976
89- *Sapindus*	*saponaria* L.	Prado et al., in press a
90- *Sapium*		Cabrera, 1976
91- *Schinopsis*	*brasiliensis* Engler [Bol.]	Meyer & Barkley, 1973

92- *Schoepfia*	*brasiliensis* DC.	Sleumer, 1984
93- *Sebastiania*		Cabrera, 1976
94- *Seguieria*	*aculeata* Jacq.	Rohwer, 1982
95- *Senna*		Irwin & Barneby, 1982
96- *Serjania*	*glabrata* Kunth	Radlkofer, 1956
97- *Sesbania*	*exasperata* Kunth	Burkart, 1952
98- *Sida*	*cordifolia* L.	herbarium specimens
99- *Sideroxylon*	*obtusifolium* (Roem. & Schult.) Pennington **subsp.** *obtusifolium*	Pennington, 1990
100- *Solanum*	*granuloso-leprosum* Dunal	Prado et al., in press a
101- *Stachytarpheta*		herbarium specimens
102- *Sterculia*	*striata* S-H.& Naud.	herbarium specimens
103- *Stigma phyllum*		Niedenzu, 1928
104- *Tabebuia*	*caraiba* (Mart.) Bur.[Bol.]	herbarium specimens
Tabebuia	*impetiginosa* (Mart. ex DC.) Standley	Gentry, 1979
105- *Terminalia*		Exell, 1940
106- *Tournefortia*	*rubicunda* Salzm. ex DC.	Devoto & Rothkugel, 1942
107- *Trichilia*	*hirta* L.	Pennington, 1981
108- *Vitex*		Troncoso, 1974
109- *Ziziphus*		Escalante, 1946

nucleus' of the Pleistocenic Arc: 11.77% of Caatingas species appear in the piedmont deciduous forests of 'Palo blanco' and 'Tipa-Pacará' in SW Bolivia-NW Argentina, and about 55% of the genera, whereas the '2nd nucleus' shares about 15% and 55% respectively. While there are no differences at generic level in the last two cases, there is a sizeable difference at specific level. However, it should be emphasized that the '2nd nucleus' is basically an artifact devised here to facilitate the analysis, since it comprises an area which although subjected to a single type of climate, groups very different geological substrata – Pre-Cambrian rocks in Misiones and E Paraguay, alluvial and æolian sedimentary areas, and calcareous outcrops as those of Corumbá and N Paraguay in the Apa river region– and also fundamentally different types of plant communities. It is beyond the scope of this study to try to analyze the vegetation of this sector to delimit the units enclosed and consequently pinpoint those which are floristically closer to the Caatingas, although obviously those on calcareous outcrops show the stronger links (Ratter et al., 1988b). In contrast, the Subandean Piedmont Forests comprise only two forest subtypes: the 'Palo blanco' and 'Tipa-Pacará' Forests. These are floristically very close to each other and only distinguishable because of a latitudinal impoverishment. Together they constitute a well-defined phytogeographic unit (Cabrera, 1976), clearly detached from the Chaco *s.s.* vegetation and the upland wetter subtropical forest (Meyer, 1963; Vervoorst, 1982). In this case, therefore, the comparison with the Caatingas flora is more realistic since the '3rd nucleus' involves a much smaller area and only one definite formation.

The phytosociological analyses undertaken in the present study (Ch. 6) agree with Cabrera (1953 & 1976) and confirm that the Subandean Piedmont Forests (*sub* 'Transitional Forests' or 'Bosques de Transición' in the Argentine literature) cannot pertain to the Chaco province, and indeed Cabrera & Willink (1980) grouped them in their Amazonian Dominium. Since, however, the Caatingas province is floristically closer to the Subandean Piedmont Forests than to the Chaco, having in common with the former not only an appreciable number of woody species, but also some that are very important and sometimes dominant in both formations (i.e. *Anadenanthera colubrina* var. *cebil* ,*Pterogyne nitens* , *Tabebuia impetiginosa* , *Astronium urundeuva* , *Myroxylon balsamum*,

TABLE 8.4: **Number of species and genera in common between the Caatingas and the Chaco *s.s.*, the Subandean Piedmont Forests and the vegetation of the Paraguay-Paraná river system.** Figures of species and genera in common are also expressed as percentages of the Caatingas totals.

		CHACO *s.s.*		SUBANDEAN PIEDMONT FORESTS (3rd nucleus)		PARAGUAY-PARANA RIVER SYSTEM (2nd nuc.)	
		Nº common	%	Nº common	%	Nº common	%
CAATINGAS	SPECIES (433)	3	0.69	51	11.77	66	15.24
	GENERA (199)	42	21.11	109	54.77	109	54.77

Amburana cearensis , *Piptadenia viridiflora* , etc.), it can be concluded that there is no reason to retain the Caatingas province within the Chaquenian Dominium, as proposed by Cabrera & Willink (1980). On the contrary, on this evidence, it should logically be grouped within their own concept of the Amazonian Dominium (*sensu* Cabrera & Willink, 1980). Consequently, these authors hierarchical classification of Latin America vegetation should be modified as follows:

II- Región Neotropical	**II- Neotropical Region**
C- Dominio Amazónico	C- Amazonian Dominium
1- Provincia Amazónica	1- Amazonian Province
2- Provincia Pacífica	2- Pacific Province
3- Provincia de los Yungas[4]	3- Yungas Province
4- Provincia Venezolana	4- Venezuelan Province
5- Provincia de los Cerrados	5- Cerrados Province
6- Provincia Paranense[5]	6- Paranense Province
7- Provincia de los Llanos[6]	7- Llanos Province
8- Provincia Atlántica	8- Atlantic Province
9- Provincia del Páramo	9- Paramo Province
10- Provincia de las Caatingas	10- Caatingas Province
E- Dominio Chaqueño	E- Chaquenian Dominium
1- Provincia Chaqueña (*s.s.*)	1- Chaco Province (*s.s.*)
2- Provincia del Espinal	2- Espinal Province
3- Provincia Prepuneña	3- Prepuna Province
4- Provincia del Monte	4- Monte Province
5- Provincia Pampeana	5- Pampean Province

In this respect, the position sustained in this thesis finds further strong support in the numerical analyses performed in Sect. 6.2, at both specific and generic level. The Caatingas have never been

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4 'Yungas' is used in masculine rendering by the Bolivian population who coined the term (Cárdenas, 1945; Braun, 1956), instead of feminine as employed by Cabrera (1976) and Cabrera & Willink (1980).

5 Includes the 'Selva de Ribera' and the Austro-Brazilian Transitional Forest units.

6 'Sabana' province in the original; 'sabana' (=savanna) is a generic term that denominates a particular formation (*sensu* Beard, 1953), and its use for a phytogeographical province is not advisable, as it could be employed e.g. for the Cerrados province as well. 'Llanos', the autochtonous name in Colombia and Venezuela for the Orinoco plains savannas, is here recommended (see Sarmiento, 1983).

grouped with the representatives of the Chaquenian Dominium included in the analysis. On the contrary, they appear very closely related to the Subandean Piedmont Forests, and both of them to the rest of the seasonal formations of the Amazonian Dominium, with which they have formed fairly consistent clusters. There are also profound contacts between the Caatingas and the vegetation of the Guajira province.

8.3- The origin of the Caatingas flora:

It can be postulated that the Caatingas vegetation has been in the present position for a very long period, as indeed some geological evidence seems to indicate (Tricart, 1961). Nevertheless, it was also subject to the Pleistocenic wet-dry cycles, particularly in the Mata de Cipó area and central San Francisco valley, which were even drier during certain periods (Tricart, 1961 & 1985). If the Caatingas have been firmly established since the end of the Tertiary (Ab' Sáber, 1974), a marked degree of endemism would be expected in the flora and fauna. This is the case as regards plants (see preceding discussion), and although the picture is much more obscure with respect to mammals (Mares et al., 1985), it is also true for the rich endemic bird fauna (see Ch. 7). The particularly numerous endemic genera and species in the Cactaceae, a family nearly restricted to South America, also supports the hypothesis of long established Caatingas.

Nevertheless, both endemic and non-endemic plant taxa may have an alien origin within the continent. Some migratory routes (Fig. 8.3) can be postulated for the Caatingas flora from the available information in taxonomic monographs and the distribution maps presented in this thesis (Ch. 5).

a- <u>The African connection</u>: although the African-South American angiosperm connection is rather polemical (compare Raven & Axelrod, 1974, *vs.* Thorne, 1978), a number of pantropical genera could have entered South America via the Caatingas (or viceversa!) at the time of a closer relative position to Africa (Raven & Axelrod, 1974; Gillet, 1979), such as *Ziziphus* , *Cochlospermum* , *Parkinsonia* , etc.; two potential examples are analyzed below. The only known American species of *Commiphora* , a genus of some 185 species otherwise almost entirely African (a few species occur in Arabia and India), is *C. leptophloeos* ,

Fig. 8.3: Postulated migratory routes reputable for the origin of the Caatingas flora (see explanation in text).

previously recognized as *Bursera* simply because it had been collected in South America and not in Africa (Gillet, 1979). It is practically restricted to the Caatingas (Fig. 5.35) save for three clear-cut outposts indicating a previous more expanded range of the species, or even probable ancient expansions of the Caatingas themselves (see maps in Hester, 1966, *sub* 'Deciduous Forest', and Ab' Sáber, 1977b). The specimen collected by Ratter et al. in Corumbá area shows a certain degree of morphological differentiation which may result in a new taxon at varietal or subspecific level (Gillet, *in sched.* & pers. comm.). A counter-hypothesis could be raised suggesting that *C. leptophloeos* evolved independently of the African members of the genus from the *Bursera* floristic stock present in Mesoamerica and N South America. In the genus *Erythrina* , the subgenus *Erythraster* comprises 13 species, of which 11 species occur in the Old World tropics (Krukoff & Barneby, 1974). The other two consist of a Cuban endemic and *Erythrina velutina*, which occurs in the Caatingas, W Ecuador and the dry Caribbean coast and could have arrived to South America via the African representatives of the subgenus.

b- The Caribbean connection: certain species of the Caatingas seem to have derived from a close relative in the dry Caribbean coast of N Colombia and Venezuela (the Guajira province of Cabrera & Willink, 1980), with some probable cases of vicariance. This hypothesis finds support in Sarmiento (1975), who studied the arid biomes of South America and made a comparison at generic level, and concluded that the strongest floristic relationships of the Caatingas refer to the Guajira province together with the Northern Andean Valleys of Colombia. Such is the case of *Copernicia tectorum-C. cerifera* , later deriving into the southern *C. alba* (see Sect. 8.2); *Licania rigida* of the Caatingas has its closest relative in the Colombian and Venezuelan *L. arborea* (Prance, 1972), which also extends into Central America; *Spondias tuberosa* , the resourceful 'umbú' of the sertão encounters its homologous species in *S. mombin* from the dry Caribbean sector of N South America. In the Cactaceae family, the Caatingas endemic *Pereskia aureiflora* is closest to *P. guamacho* of the dry Guajira province (Leuenberger, 1986), despite the fact that for this genus an Andean route might seem more likely if the distribution of all of its species is considered. Some species seem to follow a Caatingas-Guajira disjunction in their range, such as *Mimosa*

tenuiflora and *Chloroleucon mangense* , perhaps indicating that they did not have enough evolutionary time to speciate in either area; other species would be Caatingas endemics if it were not for isolated collections in N South America, such as *Sebastiania catingae* (disjunct in Sabanilla, Colombia; see Pax & Hoffmann, 1958b) and *Mimosa gemmulata* (disjunct in Lara, Venezuela; see Barneby, 1985).

Some other examples could be provided, but sometimes the connection Guajira-Caatingas is not so clear-cut. For instance, the present author has been unable to find any literature on the genus *Cavanillesia* , or confirmation via herbarium specimens at K, but it seems most likely that *C. arborea* of the Caatingas, Mata de Cipó and forests in Espírito Santo, must be a vicariad of *C. platanifolia* , the 'macondo' of the Caribbean coast of South America, but there also appears to be a third species in Amazonian localities (Rizzini, 1963) of unknown status. Harley (in press) shows two Labiatae which link the Caatingas to Venezuela, i.e. the monotypic *Eriopidium strictum* (occurring only in NE Brazil and the Orinoco river valley), and the caatinga species *Hyptis salzmanii* with disjunction in NE Venezuela but with one collection in Guyana close to the Rio Branco area.

c- The Andean route: it is likely that some species have reached the Caatingas via the west of the continent, as the extant fragments of a previously continuous distribution indicate. The main stepping stones of this route – dry Caribbean area, coastal western Ecuador, piedmont forests of Bolivia and Argentina, and the rest of the Pleistocenic Arc – are linked via dry interandean valleys mainly in Colombia and Peru, also postulated to have been used as migratory pathways by animals (Müller, 1973). The complex *Geoffroea striata/spinosa* (Fig. 5.58), and the trees *Senna spectabilis* (Fig. 5.62), *Parkinsonia aculeata* (Fig. 5.74) and *Sideroxylon obtusifolium* (Fig. 5.75) seem to follow this pattern.

A more complex matter is to determine the direction followed by the proposed taxa for this migratory route. For instance, Haynes & Holm-Nielsen (1989) argue for the Caatingas as the possible center of origin of the genus *Hydrochleys* (Limnocharitaceae), where the greatest concentration of primitive characters is found, and postulate a southerly migration which resembles very much the Pleistocenic Arc proposed

here. Subsequently, the genus must have joined the Andean route up to the Caribbean coast of South America, and from here diverging SE to the Guianas and NW to Central America. Haynes & Holm-Nielsen (1989) point out the striking fact of the absence of Alismatidae from the Amazon basin, as most taxa are restricted to areas with wet and dry seasons, specially in ephemeral ponds and forests with flood-drought cycles. Although the Andean route in the genus *Hydrochleys* is well supported by the evidence provided, there is still a chance that a Trans-Amazonian route could also have existed, whereas any suitable environment for these aquatic plants has disappeared along the migratory pathway across eastern Amazonia. Only fossil or pollen evidence could prove this point.

Exactly the opposite direction seems to have occurred with the genus *Coursetia* sect. *Craccoides* (Leguminosae), particularly in the final leg NW Argentina-Caatingas when it runs a SW-NE orientation as proposed by Andrade-Lima (1982) but for the wrong floristic stock. Lavin (1988), in his impressive monographic treatment of *Coursetia* , makes very valuable comments on its phytogeography. He postulates that the caatinga species *C. vicioides* , the closest to the perichaquenian *C. hassleri* , must have arrived (or its ancestors) to the Caatingas from the south, migrating from N Argentina and S Bolivia where there are a number of species pertaining to the same sect. *Craccoides* . This section has two primary centers of diversity in the cordilleras of central and southern Mexico and in the Andes of Colombia to N Peru, basically following the Amphitropical Seasonal Forests Pattern shown in Sect. 5.3.3 . Lavin found the presence of *Coursetia rostrata* (sect. *Coursetia*) in the Caatingas rather puzzling since it is here very distant from its closest relatives, the *C. glandulosa* group in Mexico, and he suggested it must have migrated into NE Brazil via N Argentina and S Bolivia. However, an alternative scenario is that a common ancestral stock could have migrated together with other members of the flora of Mexico, either elements of the Sonora desert (*Parkinsonia aculeata* , *Sideroxylon obtusifolium*) or deciduous forests communities (*Tabebuia impetiginosa* , *Coutarea hexandra* , *Crateva tapia* , *Myroxylon balsamum* , *Poeppigia procera* , etc.; see Sect. 5.3.3), via a Trans-Amazonian route (see below).

d- The Trans-Amazonian route: a number of Caatingas species probably have arrived there via the Atlantic side of the continent, crossing the Amazonian plains at a time when the rainforests had receded because of the wet-dry cycles during the Pleistocene. Originally coming from Mexico, Central America and/or the Caribbean area, the main stepping stones of this route seem to be: 1- the Guajira province in N Colombia and Venezuela, and the Orinoco delta in some cases; 2- the Guianas as a whole, or the SW sector of Guyana and adjoining Rio Branco in Brazil, i.e. the Roraima-Rupununi area where *Commiphora leptophloeos* , *Brunfelsia uniflora* and *Coursetia ferruginea* have been collected; 3- the Faro-Monte Alegre area near Santarém in Pará, Brazil, where species such as *Tabebuia impetiginosa* (Fig. 5.70), *Myroxylon balsamum* (Fig. 5.71), *Aspidosperma pyrifolium* (Marcondes-Ferreira, 1988) and *Cereus* cf. *jamacaru* (Andrade-Lima, 1959 & 1966c) have been collected or cited; 4- several localities in Maranhão state, such as the alleged caatinga vegetation in the Coroatá-Vargem Grande area (Bigarella et al., 1975); and 5- finally the province of the Caatingas. Some of these species would extend from there to the south into SE Brazil or E Paraguay, therefore overlapping in part the Pleistocenic Arc (see Sect. 5.3.1), and in some cases even reaching the savannas of NE Bolivia (Llanos de Mojos).

The present author must disagree with Lavin (1988) when he denies the possibility of an ancient E Amazonian extension of the Caatingas during a drier climatic phase. On the contrary, several distribution maps shown in this thesis present basically the evidence of such an expansion, of which only relictual isolated populations are extant at present. This does not invalidate his hypothesis of the arrival of *Coursetia rostrata* via the Andean route (see above), but it is here considered as more likely that the Trans-Amazonian route was taken instead, even though the evidence for this has been wiped out by the expansion of the rainforests. Perhaps significantly, there is also mounting evidence from animal distribution patterns for Amazonian cross-connections (see Ch. 7, and Müller, 1973).

The most relevant species following this route apparently also migrated via the Andean route, and they are commented upon below (point **e**). Some other examples probably are the distribution ranges of *Crateva tapia* (Fig. 5.68), *Hymenaea courbaril* var. *courbaril* (Fig. 5.69),

Albizia polyantha (Fig. 5.91), and *Aspidosperma discolor* (Fig. 5.92). Iltis (1959) in his landmark paper on the taxonomy and evolution of *Cleome* sect. *Physostemon* provided further evidence for this route. The Caatingas species, *C. tenuifolia* and *C. rotundifolia* , are considered highly evolved taxa, and their ancestral stock in all likelihood has come from W Mexico via this Trans-Amazonian route, as *C. guianensis* (a wide ranging species in the Americas, collected in Monte Alegre, Pará, and in the driest 'seridó' of Paraiba) and *C. lanceolata* clearly suggest, the latter species with three subspecies in Oaxaca (Mexico), the Caatingas and E Paraguay.

e- The pincers movement (Andean/Trans-Amazonian route): a group of species of deciduous seasonal forests seem likely to have migrated following both preceding pathways, unless some sectors of their present distribution consist of much more recent arrivals which could not be attributed to Pleistocenic climatic fluctuations. Such are the cases of the amphitropical trees *Tabebuia impetiginosa* (Fig. 5.70), *Myroxylon balsamum* (Fig. 5.71), *Coutarea hexandra* (Fig. 5.67), the shrub *Ipomoea carnea* ssp. *fistulosa* (Fig. 5.59), and the South American complex *Cordia alliodora/trichotoma* (Fig. 5.64). Probably *Solanum granuloso-leprosum* (Fig. 5.63) could be added to this list, and also the genus *Loxopterigium* (Anacardiaceae) since it fragments into five species along both sides of the continent, although there is no proof that both arms of the distribution ever met in the intervening Pleistocenic Arc (Fig. 5.61).

Cochlospermum vitifolium , regarded as the most primitive species of the genus, also seems to have followed both routes (see map in Poppendieck, 1981). The cerrado species *C. regium* (an hexaploid with 2n=36; Morawetz, 1986) may have evolved from *C. vitifolium* (2n=24), and a corridor of transitional forms between them occurs to the west of the Caatingas. Meanwhile, both species meet again in Bolivia, but in this case they are in distinct habitats and do not appear to hybridize. This is taken here as an indication that both routes were followed independently, although not necessarily simultaneously. Thus the eastern arm gave rise to *C. regium* when it had to face the very different environment of the Cerrados, and it thereby spread south until eventually meeting the disjunct populations of *C. vitifolium* in Bolivia. This agrees with

Poppendieck's view (op. cit.) that these latter populations are a relict of a once continuous distribution previous to the evolution of *C. regium* , and also with Morawetz (1986) who postulates the origin of polyploidy in *Cochlospermum* as a result of repeated migrations and/or changes of ecological niche.

The section *Franciscea* in the genus *Brunfelsia* (Solanaceae) recognizes two major centres of speciation: the eastern Andes, with the more primitive species, and SE Brazil, with the greatest number of species (Plowman, 1979). The bridge between both areas is *Brunfelsia uniflora* (Fig. 5.56), which migrated either East from the Andes in the Piedmont Forests to SE Brazil and later the Caatingas, or from SE Brazil westwards and northwards, but in any case the corridor must have been available through the wet-dry arc of seasonal vegetation. From the Caatingas this species very probably extended north to the dry Guajira province in the Caribbean coast of South America through E Amazonia, leaving extant populations in the Rio Branco-Roraima region. The latter "are morphologically distinct and appear to have been isolated in this endemic area for some time" (Plowman, op. cit., p.488). Thus, the section *Franciscea* seems to adjust well to the pincers movement, while the particular case of *B. uniflora* can be taken as further evidence of the Trans-Amazonian route, in this case probably in S-N direction.

Another group of Caatinga species seems to have moved along this proposed migratory route but either failed to complete the pincers movements or they became extinct in certain parts of it. Such is the case of *Aspidosperma cuspa* and *A. polyneuron* (Fig. 5.54 & 5.55), which in the west side of the continent spread through dry Andean valleys in Colombia but only reaching Ecuador or N Peru, and both are absent from Bolivia or the Subandean Piedmont Forests. Also *Erythrina velutina* can be mentioned, which reaches as far south as W Ecuador in the west, and the Caatingas in the east (see distribution map in Bigarella et al., 1975). Another example is provided by the Composite herbaceous genus *Isocarpha* , which presents five species arranged in two sections (Keil & Stuessy, 1981). Section *Isocarpha* holds four of the species, two occurring from Mexico to N Colombia and Venezuela through Central America and the West Indies, while the other two appear at different altitudes in the lowlands of W Ecuador (*I. microcephala* , confined to the

strongly Caatingas-linked vegetation of this area) and the mountains of N Peru. The sect.*Cylindriflorae* contains only the Caatingas endemic *I. megacephala* , which has substantially differentiated evolutionarily from the rest of the genus (Keil & Stuessy, 1981). The latter species and section would be totally isolated and disjunct if it were not for two exsiccata of *I. atriplicifolia* var. *atriplicifolia* in N Piauí and N Maranhão, at the edge of the Caatingas, while the nearest collections of this variety are located in the Maracaibo Lake in Venezuela and dry coastal Colombia (the Guajira province).

f- The Pleistocenic Arc as a migratory route: a considerable group of woody species, comprising some of the more important members of the Caatingas, follow this pattern of distribution across central South America, as discussed at length in Sect. 5.3.1. This arc of formations must have been used as a migration corridor by other amphitropical and South American species (see routes **c**, **d** and **e**). *Anandenanthera colubrina* var. *cebil* (Fig. 5.38), the paradigm of this kind of distribution, is complemented by *A. colubrina* var. *colubrina* (Fig. 5.39) which is supposed to have arisen from var. *cebil* or an ancestral form (Altschul, 1964) in the Planalto of central Brazil, where the greatest variability of this small genus concentrates. The other species of the genus, *A. peregrina* , must have originated at an earlier time than *A. colubrina* itself (Altschul, 1964) in the same area, and it seems to have migrated northwards via the Pleistocenic Arc and either the Trans-Amazonian route or 'campos' expansions amid the then contracted Amazon rainforests, to finally arrive in N Venezuela and the West Indies.

The extra-Amazonian Phytolaccaceous genera *Seguieria* and *Gallesia* seem to have their centre of diversity and probably of origin in SE Brazil, although Rohwer (1982, p. 243) has misgivings about this view. Five of the six species of *Seguieria* seem to fall within the scope of the Pleistocenic Arc, from wetter areas in the Caatingas to N Peru, particularly *Seguieria aculeata* which also extends beyond this arc to the Guajira province (see Rohwer, 1982, Fig. 11). Some of these species, or their ancestors, must have used the seasonal formations as a corridor to finally speciate in NW Bolivia (*S. brevithyrsa*) or N South America (*S. macrophylla*).

g- The Amazonian encroachment: a more reduced group of species pertaining to genera which have the bulk of their distribution in the Amazon rainforests and related formations (such as gallery forests in the Cerrados), can also be found well into the semiarid NE Brazil. Examples are *Couepia uiti* (Fig. 5.93), and in the mainly Amazonian genus *Sterculia* (Taroda, 1984), *S. striata* occurs in arboreal caatinga (Andrade-Lima, 1975; Ratter et al., 1978) and also in W Bahia, N Minas Gerais and the Corumbá calcareous outcrops (Fig. 5.53). The Leguminous tree *Poeppigia procera* extends from Mexico and Central America to Andean South America, but instead of following the usual pattern of seasonal formations seems to take a shortcut through the Amazon (Fig. 5.72) to later reappear in the Caatingas. The small Amazonian genus *Martiodendron* (Leguminosae) comprises mostly majestic canopy trees but also a shrub to treelet which has evolved in northern areas of the Cerrados and in the Caatingas, *M. mediterraneum* (Koeppen & Iltis, 1962).

h- The Atlantic forest encroachment: in Rizzini's view (1963, 1979) half the floristic stock of the Caatingas is derived from the Mata Atlântica rainforests. It is not possible with the available taxonomic and evolutionary information to ascertain the correctness of this view, but there exist evidence indicating that certain species could possibly have resulted from adaptation of taxa from more humid environments. Lee & Langenheim (1975) suggest that the genus *Hymenaea* (Fabaceae) has originated in rainforests in the New World, probably with *H. oblongifolia* in the center of diversification of present-day species. One of the varieties of that species, var. *latifolia* of the 'Hylaea Bahiana' (Andrade-Lima, 1966a), probably gave rise to the caatinga endemism *H. eriogyne* , together with other species. Likewise, the Caatingas endemics *Pereskia bahiensis* and *P. stenantha* (Cactaceae) are very close to, and probably derived from, *P. grandifolia* of coastal Brazil (Leuenberger, 1986). Also in the Fabaceae, the caatinga endemic *Parapiptadenia zehntneri* is closest to *P. pterosperma* of the Atlantic rainforests in Espírito Santo and Rio de Janeiro (Lima & Lima, 1984); a parallel situation is reported for *Luetzelburgia* (Lima, 1984), where the Caatingas endemic *L. andrade-limae* is the nearest to *L. guaissara* from Mata Atlântica in Rio de Janeiro, São Paulo, Paraná and Santa Catarina. A number of species accepted here as albeit rather dubious members of the Caatingas have

very probably edged into that province from the Atlantic forests or the local 'brejos' in wetter years or taking advantage of somewhat more humid pockets. Such taxa are *Phyllosthylon brasiliense* , *Gallesia integrifolia* , *Seguieria aculeata* , *Myroxylon balsamum* , *Pisonia tomentosa* , etc.. The Atlantic forest- Caatinga link has not been explored intensively in the present study.

i- The Cerrados expansions: some species whose distribution is basically centered in the Cerrados savannas of central Brazil, can also extend to NE Brazil and become relevant members of the Caatingas, such as *Tabebuia caraiba* (Fig. 5.52). Nevertheless, in most such cases their presence in the thorn forests seems to be more occasional, e.g.: *Machaerium acutifolium* (Fig. 5.80), *Platypodium elegans* (Fig. 5.65), *Hymenaea martiana* (Fig. 5.79), *Copaifera langsdorfii* and *Aspidosperma discolor* (Fig. 5.92), the latter also extending into the Amazon forests. Also *Riedeliella graciliflora* is a cerrado shrub with disjunct populations in the Caatingas of SW Bahia (Lima & Vaz, 1984).

j- Some curious distributions: two perplexing cases of disjunction have been found during the course of this study. The Apocynaceae *Skytanthus hancorniifolius* has been recorded in the Caatingas (Harley & Mayo, 1980), whereas the other species of this genus are known to occur in the N Chilean desert. Very similar to this pattern is the distribution of *Hyptis* sect. *Leucocephala* (Harley, in press) which comprises three species: *H. leucocephala* is a small herb endemic to the Caatingas, *H. stachydifolia* is a shrub of 'campo rupestre' upland areas in N Bahia, while on the other side of the continent their closest relative, *H. elongata* , occurs in coastal Peru. These enormous disjuncts Caatingas-coastal Pacific desert of Peru and Chile are regarded here as very puzzling, and no discussion to this kind of disjunction has been encountered. It could be, obviously, the result of somewhat modern long-distance dispersal (migratory birds carrying their seeds?, across the Andes??), or both areas had been connected somehow before the final uplift of the Puna Altiplano in the late Tertiary (Pliocene, see Solbrig, 1976), or they are relictual fragments at the extremes of some of the NE Brazil-Andean Cordillera distributions previously discussed.

8.4- Distribution patterns and palæoclimates:

The individual species distribution dot maps presented in sections 5.3.1, 5.3.2 and 5.3.3 have been superimposed to produce two compound maps (Fig. 8.4 & 8.5) which aim to show the main distribution patterns which are at the heart of the discussion and analyses presented in this thesis. Fig. 8.4 maps the distribution 'tendencies' or patterns of those 36 species judged to comprise what has been called here the 'Residual Pleistocenic Seasonal Formations Arc', or Pleistocenic Arc (see legend for list of species involved, and their individual distribution maps in Sect. 5.3.1). Three concentrations or 'nuclei' of distributions can be discerned: (1) the Caatingas of NE Brazil, (2) the Paraguay-Paraná river system, and (3) the Subandean Piedmont Forests of SW Bolivia and NW Argentina. Less dense dotting is visible expanding to the west of the 1st nucleus into Maranhão state, where the presence of relictual caatinga outposts is still a controversial matter (cf. Galvão, 1955, and Bigarella et al., 1975, vis-à-vis Eiten, 1965 & 1972, p. 288). This area in turn can be hypothesized as linking to the Faro/Monte Alegre area in Pará, and further north to the Roraima-Guyana border area. The single dot shown in the latter region corresponds to the very significant exsiccatum of *Commiphora leptophloeos* by E. Ule.

The first nucleus is somewhat less loosely connected to the second through two 'tracks'[7]: the northern and the southern routes. The northern track seems to cut present-day Cerrados in two halves, extending as a narrow strip from W Bahia (probably getting into Goiás via the Rio Grande valley) to the calcareous outcrops in the Federal District and surrounding areas (see Ratter et al., 1978). The deciduous forests of the so-called Mato Grosso de Goiás (beginning somewhat to the E of the city of Goiânia) are part of this track, which crosses the Araguaia river at the height of Aragarças, presumably here branching north to the Xavantina/Cachimbo and Ilha do Bananal areas, and west to the Cuiabá-N Pantanal area, later reaching the calcareous hills around Corumbá and Urucúm in Mato Grosso do Sul (Kanter, 1936; Kuhlman, 1954; Ratter et al., 1988b).

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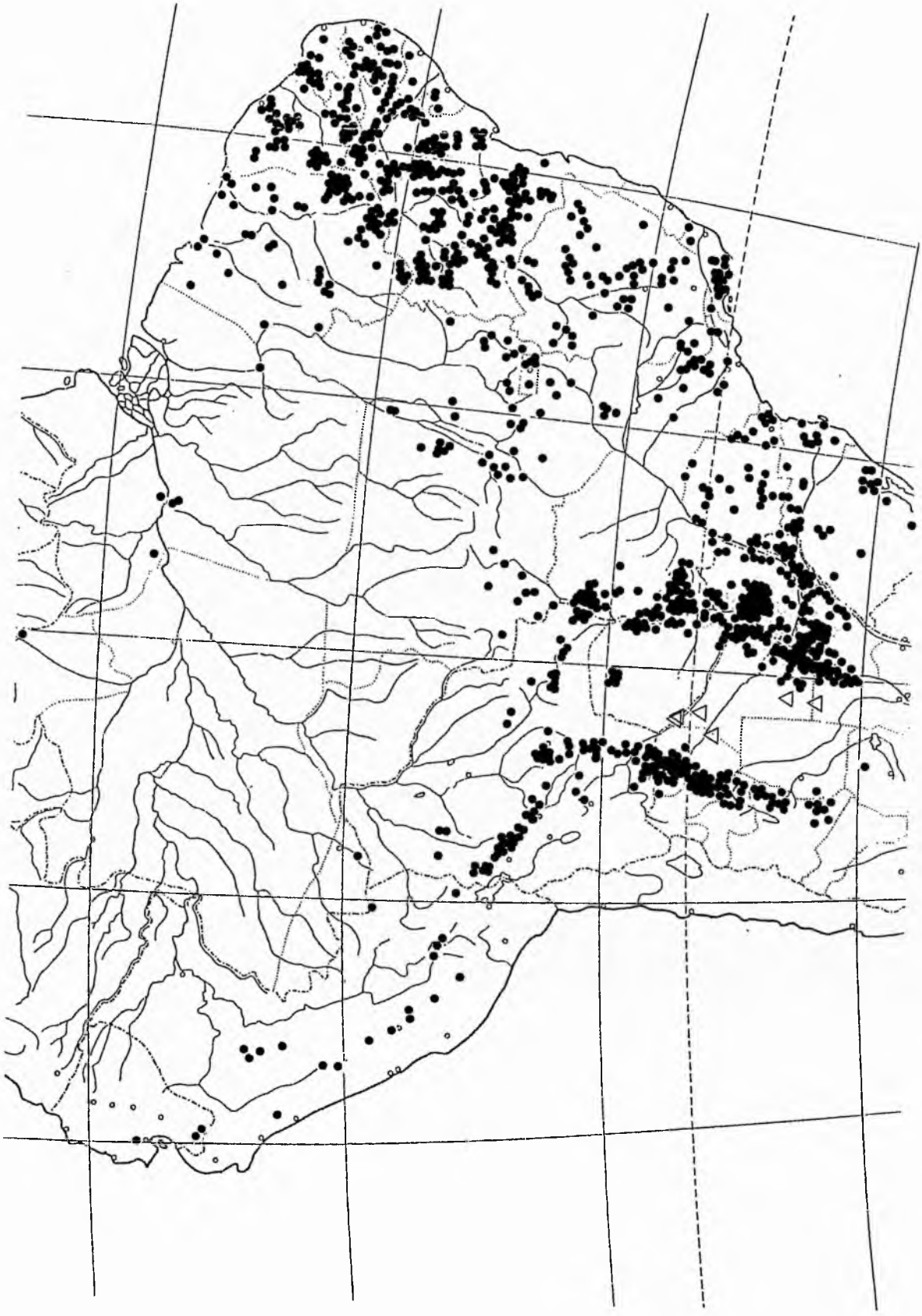
[7] The present author is aware that some of the proposed 'tracks' might simply overlap with well collected areas or routes, instead of indicating an adjusted pattern of distribution. However, it is here believed that these tracks do suggest ancient connections between the nuclei of distribution.

Fig. 8.4: Compound map of the 36 woody species following wholly or in part the Pleistocenic Arc of distribution. Open triangles indicate the few intrusions of tropical elements into the Chaco plains. The species mapped are: *Alseis floribunda, Amburana cearensis, Anadenanthera colubrina* var. *cebil* and var. *colubrina, Aspidosperma pyrifolium, Aspidosperma riedelii* ssp. *riedelii* and ssp. *oliganthum, Astronium balansae, A. concinnum, A. urundeuva, Athyana weinmannifolia, Balfourodendron riedelianum, Brunfelsia australis, Calycophyllum multiflorum, Carica quercifolia, Celtis pubescens, Combretum leprosum, Commiphora leptophloeos, Diatenopteryx sorbifolia, Diplokeleba floribunda, D. herzogii, Enterolobium contortisiliquum, Hymenaea martiana, H. velutina, Machaerium acutifolium, Maytenus ilicifolia, Mimosa caesalpiniifolia, Patagonula americana, P. bahiensis, Phytolacca dioica, Piptadenia viridiflora, Pouteria gardneriana, Pterogyne nitens, Ruprechtia laxiflora, Schinopsis brasiliensis, S. peruviana, Ziziphus guaranitica, Z. oblongifolius.*



The southern track extends at first along the São Francisco and Jequitinhonha river valleys, and south in a wide band along the Rio das Velhas up to Belo Horizonte area and the Rio de Janeiro state. The latter region has been subject to intense wet-dry climatic fluctuations during the Pleistocene (Cailleux & Tricart, 1959;Tricart, 1961). The southern track then goes through the states of São Paulo, Paraná and Santa Catarina, mostly via the Planalto and river Uruguay basin forests, until meeting the 2nd nucleus of distribution in NE Argentina, E Paraguay and SW Mato Grosso do Sul.

The 2nd nucleus, with a central axis in the Paraguay-Paraná system is nowadays linked to the 3rd nucleus only through the Santiago and Chiquitos Sierras in Bolivia. This connection is interrupted between Chiquitos and Santa Cruz de la Sierra by a moderate northwards protrusion of the Chaco *s.s.* (see Fig. 8.2), which seems to encounter or to give way to tropical forests of direct Amazonian influence with no intervening communities of species of the Pleistocenic Arc. It is likely, however, that there were almost certainly additional links in the past between the 2nd and 3rd nuclei, as is today exemplified by the vegetation of the Cerro León in the middle of the Paraguayan Chaco plains. Spichiger & Ramella (1989) and Ramella & Spichiger (1989) describe some communities on these hills and along the Timane/Lagerenza river valley, which very closely resemble the physiognomy and floristics of both the 'Palo blanco' forest and arboreal caatinga, being also very similar to the 'caatinga' forest of calcareous hills around Corumbá (Ratter et al., 1988b). It is likely that when the flora and vegetation of Cerro León becomes better known, stronger links with calcareous and Caatingas vegetation will emerge. Indeed, one would predict the presence of at least some species, such as *Schinopsis brasiliensis* , *Commiphora leptophloeos* , *Tabebuia impetiginosa* , *Piptadenia viridiflora* , *Senna spectabilis* var. *spectabilis* , *Ruprechtia laxiflora* , *Enterolobium contortisiliquum* , *Patagonula americana* , one of the species of the genus *Loxopterigium* (or a new taxon), the complex *Cordia alliodora/ trichotoma* , *Phyllost ylon rhamnoides* , or even *Brunfelsia uniflora* , *Myroxylon balsamum* or *Aspidosperma polyneuron* , none of which have been cited for the area yet. Any of these taxa would add to the already known presence there of *Anadenanthera colubrina* var. *cebil* ,

Astronium urundeuva , *Amburana cearensis* , *Pterogyne nitens* , *Geoffroea striata* , *Aspidosperma pyrifolium* , *Albizia polyantha* , *Maclura tinctoria* , *Pisonia zapallo* , *Sideroxylon obtusifolium* and *Calycophyllum multiflorum* (Spichiger & Ramella, 1989; Ramella & Spichiger, 1989). It is also likely that specific and even generic endemisms would be encountered in the Cerro León or other isolated hills of the Paraguayan Chaco, such as the recently described and puzzling *Sphingiphila* (Bignoniaceae), known only from the type collection in the Cerro Chovoreca in N Paraguay (Gentry, 1990).

The 3rd nucleus stretches continuously from SE Catamarca in NW Argentina to Santa Cruz de la Sierra in Bolivia as a narrow strip of deciduous forests. It extends tenuously but persistently along the foothills of the Andes in NW Bolivia, and enters Peru to be present in dry interandean valleys and just reach western Ecuador. The Acre state in Brazil has two species of the Pleistocenic Arc (*Amburana cearensis* var. *acreana* and *Celtis pubescens*) and, not unexpectedly, other more widespread species have also been collected in this area, e.g. *Myroxylon balsamum* and *Poeppigia procera* .

The composite map of Fig. 8.4 also shows a conspicuous blank area between the 2nd and 3rd nuclei, which corresponds to the Chaco s.s. as here defined (see Fig. 8.2). This is further striking evidence of the virtual lack of floristic links between the Chaco and the Caatingas. There are, however, six exsiccata within the Chaco (indicated with open triangles in Fig. 8.4) which correspond to some of the few intrusions of tropical elements in the Chaco plains via the gallery forests in the west (*Enterolobium contortisiliquum* , *Calycophyllum multiflorum* , *Albizia polyantha* , *Anadenanthera colubrina* var. *cebil*), and via gallery forest or relictual stands of richer forest in the east (*Ruprechtia laxiflora* , *Patagonula americana* , *Phytolacca dioica* , *Astronium balansae*). The scanty presence of these elements within the Chaco plains, together with those cited in Morello (1967), Adámoli et al. (1972) and Morello & Adámoli (1974), were regarded by the same authors as 'species of non-chaquenian lineage' (Adámoli et al., 1972) or 'transchaquenian elements of subtropical forests' (Morello & Adámoli, 1974, p. 44). In Table 8.5 are listed some species of the 'Palo blanco' and 'Tipa-Pacará' forests whose

TABLE 8.5: **List of woody species of the Subandean Piedmont Forests also occasionally occurring in Western Chaco.**

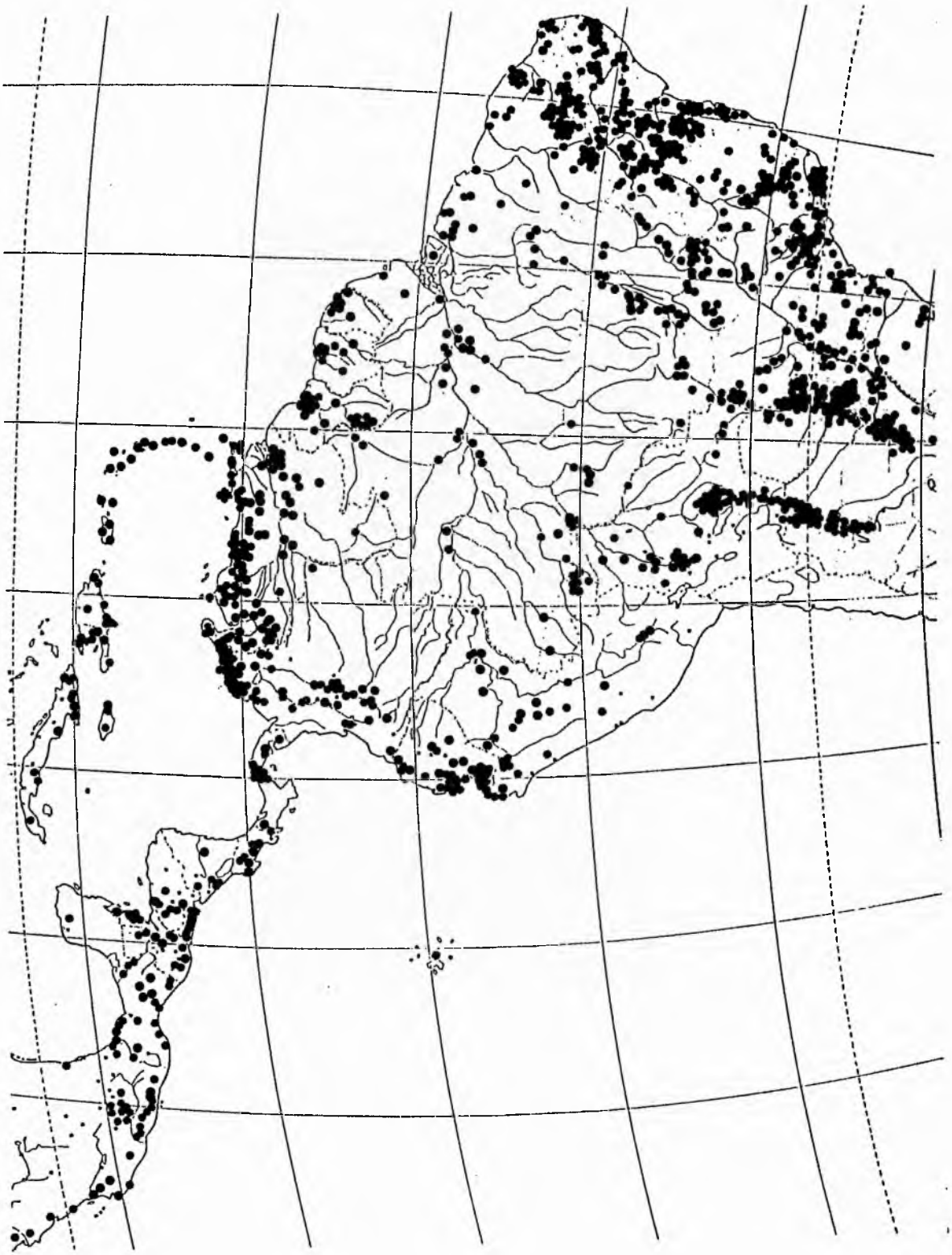
Anadenanthera colubrina (Vell.) Bren. **var.** *cebil* (Griseb.) Altschul
Basistemon spinosus (Chodat) Moldenke
Calycophyllum multiflorum Grisebach
Carica quercifolia (St.-Hil.) Hieron.
Ceiba chodatii (Hassler) Gibbs & Semir comb. ined.
Coursetia hassleri Chodat
Enterolobium contortisiliquum (Vell.) Morong
Jacaratia corumbensis Kuntze
Maclura tinctoria (L.) Don ex Steudel **subsp.** *mora* (Griseb.) V.Ávila
Manihot guaranitica Chodat & Hassler **subsp.** *guaranitica*
Patagonula americana L.
Pereskia sacharosa Grisebach
Phyllostylon rhamnoides (Poisson) Taubert
Pterogyne nitens Tul.
Ptilochaeta nudipes Grisebach
Quiabentia pflanzii (Vaupel) Berger

presence within the Western Chaco are further evidence that these forests were more extended to the east of their present position during the climatic fluctuations of the Pleistocene (Vuilleumier, 1971; Ab' Sáber, 1977b). These forests must have extended further south as well, as the relictual presence of *Anadenanthera colubrina* var. *cebil* in the Córdoba hills (Hunziker, 1973) seems to indicate.

Figure 8.5 presents another composite map of species relevant to the Caatingas with more ample distributions (see legend for list of species, and individual maps in Sect. 5.3.2 & 5.3.3). This map still permits a clear delimitation of the Pleistocenic Arc, and although the three nuclei of distribution are still discernible, this aggregation of species emphasizes the connecting tracks between them and also highlights links to the Caribbean and W Ecuador areas. Some of these additional species emphasize the importance of the Acre region in the west of Amazonia, whilst in the east the Faro/Monte Alegre and the Rio Branco/Roraima areas are better defined as a potential connecting route Caatingas-Guajira province; there is also an alternative route via the Guianas. A nucleus in W Ecuador is seen as linked to N Colombia through the Magdalena and Cauca valleys, as also postulated for animal distributions by Müller (1973). A number of elements reach the dry Caribbean area through Mesoamerica, coming from as far Mexico and W Central America, while others arrive to South America through the West Indies (e.g. *Hymenaea courbaril* var. *courbaril*).

It can be noted at this point that there is a close correspondence between these two synthetic maps (Fig. 8.4 & 8.5), and the hypotheses of past climatic events occurring during the Pleistocene, as exemplified in the maps and hypotheses presented by Ab' Sáber (1977b & c). Firstly, the Ab' Sáber map (Fig. 8.6; Ab' Sáber, 1977c) of Morphoclimatical and Phytogeographical Dominia of South America shows, to a certain extent, the pattern of the Pleistocenic Arc. Ab' Sáber delimited the main core areas in South America as those with homogeneous geomorphological and climatological features which correlated with known floristic provinces. His 'Domínio do Chaco Central' is then a perfect match to the Chaco *s.s.* (cf. Fig. 8.2 & 8.6), even to the extent of leaving the so-called Eastern Chaco as a transitional sector. He also regarded the 'Domínio das Caatingas' core area as perfectly defined because of its homogeneity

Fig. 8.5: Compound map of the woody species following wholly or in part the South American and Amphitropical Seasonal Forests patterns of distribution. The species mapped are: *Aspidosperma cuspa, A. polyneuron, Astronium fraxinifolium, Brunfelsia uniflora, Cordia alliodora/trichotoma* complex, *Coutarea hexandra, Crateva tapia, Geoffroea striata/spinosa* complex, *Hymenaea courbaril* var. *courbaril* and var. *stilbocarpa, Ipomoea carnea* ssp. *fistulosa,* the genus *Loxopterigium, Myroxylon balsamum, Peltophorum dubium,* the genus *Phyllostylon, Platypodium elegans, Poeppigia procera, Senna spectabilis* var. *spectabilis* and var. *excelsa, Solanum granuloso-leprosum, Tabebuia impetiginosa.*



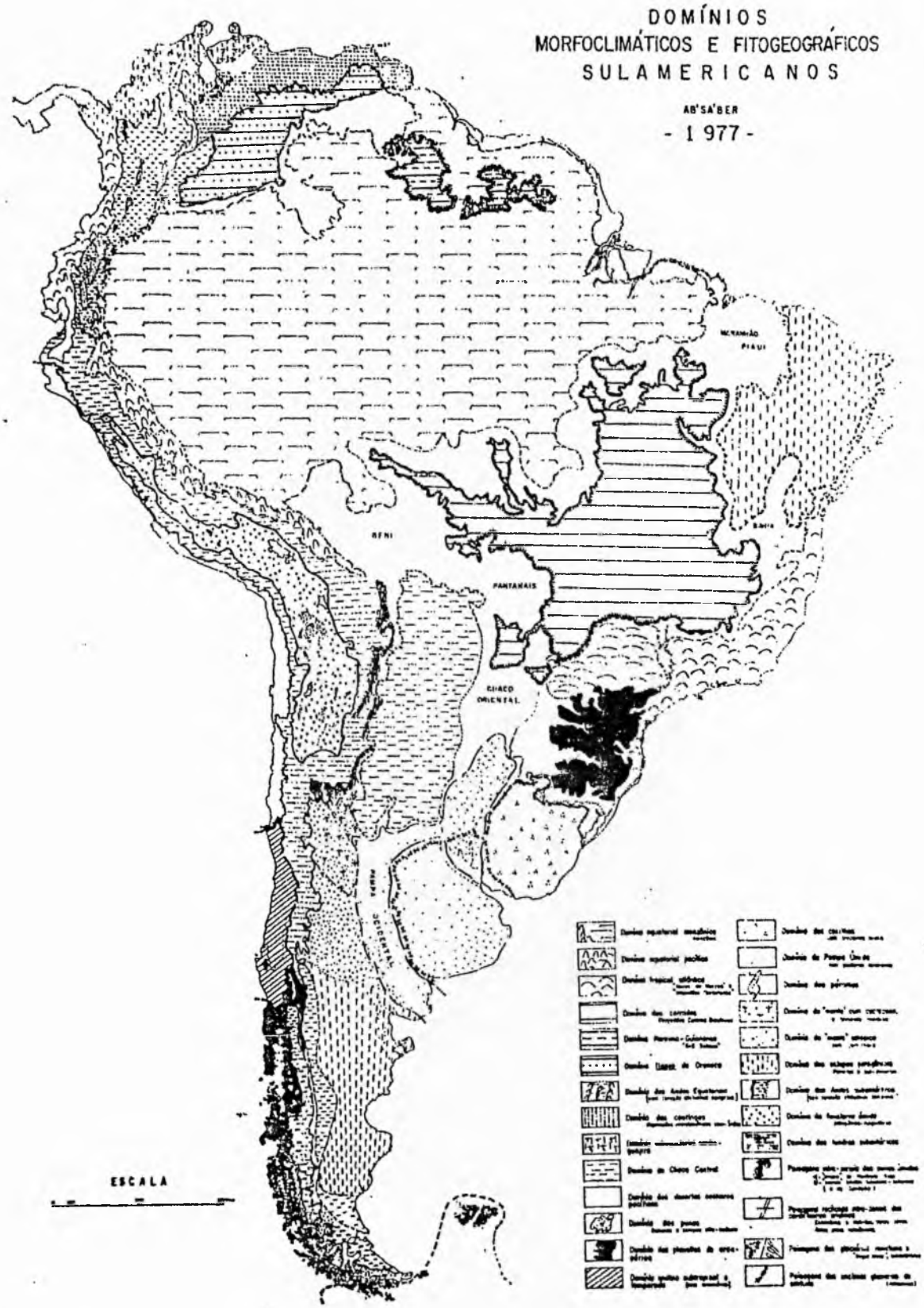


Fig. 8.6: The Morphoclimatical and Phytogeographical Dominia of South America, according to Ab' Sáber, 1977c.

in landscape, ecology and hydrology (Ab' Sáber, 1977c, p. 13); he also left a number of areas unmarked because they would not fit into any of the core areas, and these he regarded as transitional. In this category Ab' Sáber included the 'agreste', the 'mata de cipó' in S Bahia, and parts of Maranhão and Piauí. These transitional belts are continuous from the Caatingas, all around north and south of the Cerrados core area, to reach the Pantanal, Eastern Chaco, the areas north of the Santiago and Chiquitos Sierras, and the Subandean Piedmont Forests in Bolivia and NW Argentina. From the so-called Eastern Chaco finger-like protrusions extend along the Uruguay, Paraguay and Paraná river valleys. This sequence effectively traces the Arc of Residual Pleistocenic Seasonal Formations (compare Fig. 8.4 & 8.6), with some differences in what Ab' Sáber refers to as the Planalto forests, and with the detail that the calcareous enclaves within the expanse of the Cerrados are omitted. However, Ab' Sáber (1977c) pointed out that because of the scale of his map no attempt was made to indicate the presence of enclaves within the core areas.

Much the same close correspondence can be observed with the Ab' Sáber (1977b) map of natural dominia in South America between 13,000 to 18,000 years BP (Fig. 8.7). Based mainly in geomorphological evidence he proposed that the Caatingas-like vegetation and habitats were much more widespread at the time of glacial phases (Würm-Wisconsin), when the climate of South America must have been increasingly drier and somewhat colder than present (Damuth & Fairbridge, 1970; Vuilleumier, 1971; Bigarella et al., 1975; Ab' Sáber, 1977b). A 'Caatingas type' vegetation would at that time have extended south from its present position as a wide band across Minas Gerais and Rio de Janeiro, presumably also enclosing those areas of the continental shelf uncovered by the retreating sea waters along SE Brazil (see Ab' Sáber's map, and Vuilleumier, 1971, Fig. 2). The 'Caatingas area' also extended west through Piauí and Maranhão, encircling completely the Cerrados and stretching SW across N Goiás, Ilha do Bananal, the Federal District, mid-Araguaia river, the Cuiabá pediplane, the Pantanal, and finally encasing the Chaco in a much more reduced extension than that of present-day, limiting it in its north, east and west borders. At this time, under the prevailing climatic regime, it is also

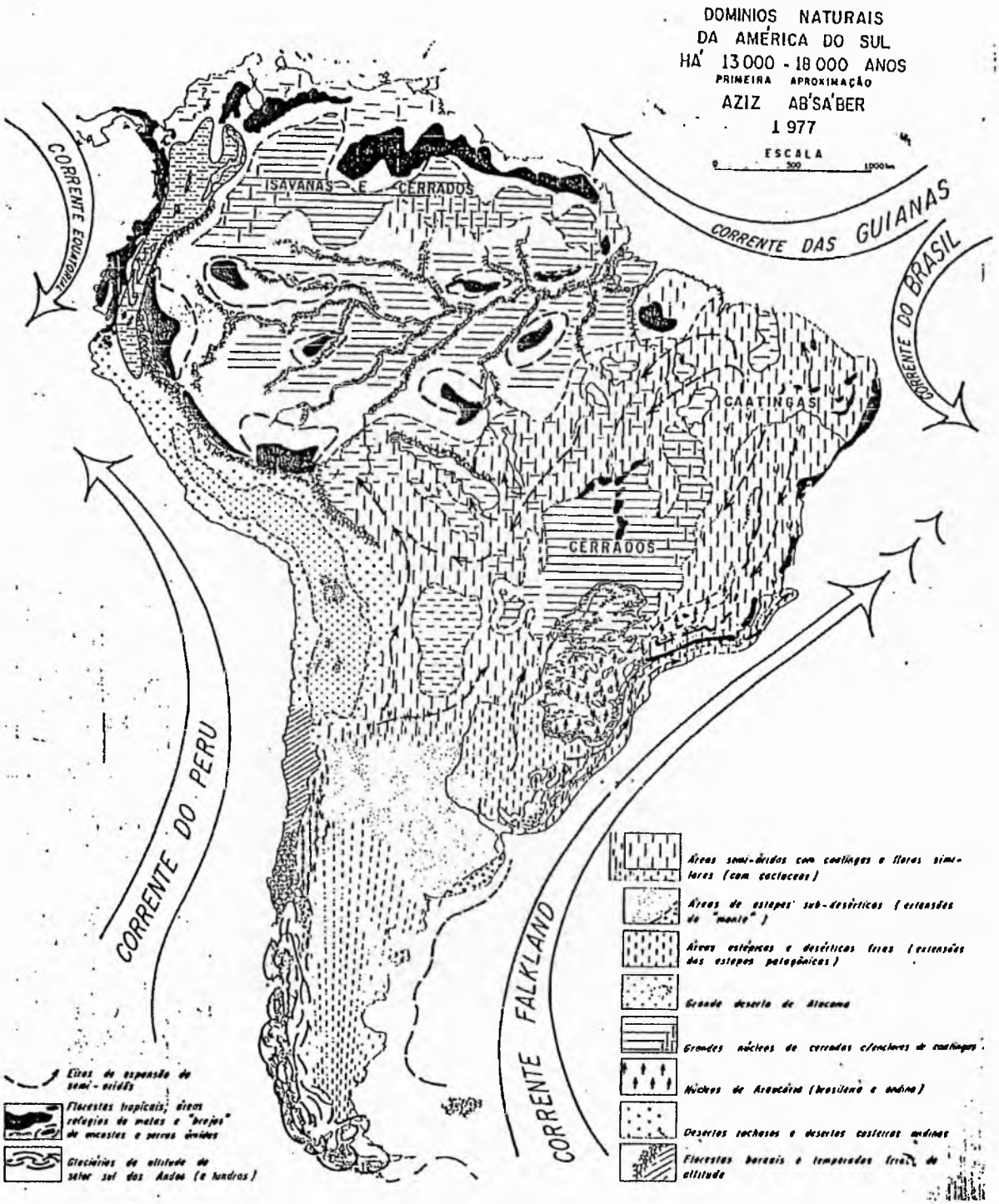


Fig. 8.7: Natural Dominia in South America between 13,000 to 18,000 years BP, according to Ab' Sáber, 1977b.

likely that the Subandean Piedmont Forests extended east into the Chaco plains.

The distribution maps of caatinga species shown in this study, and particularly the composite ones of Fig. 8.4 & 8.5, are again in close accord with Ab' Sáber hypothesis as shown in his map (Fig. 8.7). The resemblance is sustained even to the extent of precise localities (as opposed to broad regions), which were in his view, and it is here agreed, part of the Caatingas tracks not only crossing the Cerrados but also the Amazon (such as the depressions in the Rio Branco/Roraima area). There is some lack of agreement between modern distributions and these Pleistocene reconstructions. Thus, present-day plant distributions do not show strong evidence to support the wide western arm of the circum-cerrado extension of the 'Caatingas-type' vegetation as proposed by Ab' Sáber (1977b), although it could have been wiped out by climatic change and the subsequent expansion of the Cerrados and rainforests. Rather, the distribution patterns suggest that the western expansion of the Caatingas across Maranhão must have continued along eastern Amazonian areas such as Faro/ Monte Alegre, to link with the Rio Branco/Roraima depressions, SE Orinoco river delta, and finally reaching the dry Caribbean coast of N Venezuela and Colombia. In this scenario the Cerrados would have been cut into two segments, a northern one in N Goiás, S Maranhão, SW Piauí and parts of W Bahia, and a southern one in SW Goiás, S Mato Grosso, W São Paulo, and the eastern three-quarters of Mato Grosso do Sul (see Fig. 8.4). This presumably must have had an effect on the floristics of the Cerrados, and could possibly explain the N-S floristic gradient recently reported by Ratter & Dargie (in press). There would also most likely have been a track of seasonal vegetation along the Santa Catarina state, linking the coastal Caatingas and the Ilha Santa Catarina to the Paraguay-Paraná river system and cutting through the pre-existing *Araucaria* forests, via the Rio do Sul area and the upper river Uruguay, as shown here in distribution maps and also proposed by Klein (1975), together with a more southern route through Torres in Rio Grande do Sul (Klein, 1975; Ab' Sáber, 1977b). Ab' Sáber also overlooked the links that must have existed with dry western Ecuador, via dry interandean valleys both through Peru and Colombia (the Magdalena, Marañón, Huállaga, etc., river valleys),

although the Acre state area is nearly reached by one of his proposed expansions of the Caatingas.

During the interglacial episodes in the Pleistocene, temperatures were seemingly warmer than today (Vuilleumier, 1971), and the sea level rose inundating the Amazon basin and particularly the area of the Paraguay-Paraná system (see Vuilleumier, op. cit., Fig. 2).. This surely caused pronounced environmental modifications in the substratum which would have been encountered by the elements of seasonal formations reaching the latter area in the following glaciation phase, and consequently there could have been either specific differentiation or extinction for some of those elements. This view is supported by the idiosyncracies in the distributions of some taxa, e.g. *Myroxylon balsamum* and *Piptadenia viridiflora* (Fig. 5.71 & 5.48) are completely absent from the 2nd nucleus of distribution from Corumbá to Argentina, and it is also noteworthy that of all the areas of seasonal woody formations this is the only one where the genus *Loxopterigium* has not been recorded (Fig. 5.61). The shrub *Brunfelsia uniflora* (Fig. 5.56) is also absent from this area, but its place is occupied by its derivative *B. australis* (Fig. 5.57, and Plowman, 1979). Both *Amburana cearensis* (Fig. 5.40) and *Senna spectabilis* var. *spectabilis* (Fig. 5.62) seem to be suddenly interrupted in their southern expansion in the northern border of Paraguay (Apa river region). The tree *Astronium urundeuva* (i.e. =*Myracrodruon urundeuva* , Fig. 5.41) reaches Argentina along this area allegedly submitted to past marine transgressions, but it appears to be here far less frequent than in the Subandean Piedmont Forests, and ultimately it is replaced by its very close relative *A. balansae* (i.e. = *Myracrodruon balansae* , Fig. 5.83), which sometimes extends deeply into the Chaco *s.s.*. If the reinstated genus *Myracrodruon* is accepted, it would constitute a new endemism to the Pleistocenic Arc, to be added to *Amburana* , *Pterogyne* and *Patagonula* .

8.5- Tail-end:

There are still, of course, many unanswered questions. For example, if the climate was colder and drier during glacial episodes, how is it possible that caatinga-like vegetation could have extended south to NE and NW Argentina, with species which are limited by frost

occurrence?. It is possible that the same climatic features did not prevail throughout the area at the same time (Markgraf, 1989). For example, the western face of the Andes had opposite conditions to those in the east (Vuilleumier, 1971). Furthermore, it is possible that within the tropics it was relatively colder (by about 4 to 5ºC) and drier, whilst the climate in NW Argentina might have been less subject to frosts and somewhat more humid than the present climate encountered in the driest parts of the Chaco *s.s.*, so permitting the Subandean Piedmont Forests to extend their range. Markgraf's studies (1989) support this hypothesis since, according to her, moisture patterns showed regional differentiation in South America, and "the southern subtropics were substantially moister than today during full- and late-glacial times, whereas everywhere else conditions were far drier than today". In principle there seems to exist evidence that this was likely so; there are patches of lateritic palæosoils within the dry subtropical western Chaco in Formosa (Groeber, 1958), which would correspond to a past period under a humid tropical climate, which in turn left a palæofluvial system recognizable in aerial photography (Adámoli et al., 1972). On the other hand, there are dune fields in SE Bolivia, W Paraguayan Chaco and central Formosa in Argentina, nowadays immobilized and covered with vegetation, which indicate that at some stage the climate was much drier than at present (Putzer, 1962).

In the study of the distribution patterns of the Caatingas floristic elements another paradox is apparent: how do woody species such as *Albizia polyantha* , *Ipomoea carnea* ssp. *fistulosa* , *Enterolobium contortisiliquum* , *Geoffroea striata/spinosa* , *Crateva tapia* , etc., survive the capricious drought cycles of the Caatingas, whilst they are also common in areas such as the Amazon basin or the Paraguay-Paraná river system where flooding is the rule?. In this context, some results emerging from studies by F. Scarano (St. Andrews University) on anoxia tolerance are perhaps significant. Working on flooding-tolerant plants such as *Enterolobium contortisiliquum* , he established that drought causes hypoxia (low oxygen levels) in root tissues, which in turn enables the plant to prolong its flooding tolerance period (Scarano, pers. comm.).

The present study set out to critically evaluate the alleged floristic links between Chaco and Caatingas vegetation in South

America. Such links turned out to be very weak indeed, particularly when they are compared to the actual affinities between the Caatingas and other seasonal communities in the continent (the Subandean Piedmont Forests in NW Argentina and SW Bolivia, the Guajira province in N Colombia and Venezuela). Indeed, the links are so weak that it suggested that the Caatingas should be removed from the Chaquenian Dominium. Moreover, the prevailing concept of the Chaco itself, as a result of this analysis, proved to be a broad geographical entity rather than a well defined geobotanic unit in vegetational terms. The detailed study of the patterns of distribution of most of the more important species involved provides new evidence of probable ancient connections across the continent between present-day seasonal woody communities, such as what has been called here the 'Pleistocenic Arc'. These corridors of semiarid to strongly seasonal formations seem likely to have functioned as migratory routes by plant species, and this scenario provides a logical explanation for the patterns of speciation and degree of diversity found in such taxa when subsequent climatic changes broke up their previously more continuous distributions.

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